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ANATOMY OF THE GARLIC BULB AND FACTORS AFFECTING BULB DEVELOPMENT¹

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THIS INVESTIGATION on the structure of garlic (*Allium sativum* L.) was undertaken to establish a background for cultural studies on garlic as a crop plant. While garlic is one of the oldest crops under cultivation, there have been few studies on either its structure or its development under field conditions.

The data presented here are essentially descriptive; in only one or two instances were developmental studies made. All vegetative parts of the plant are described but not the seedstalks or flowers. Since any structural study should be closely related to the gross development of the plant in the field, data obtained on factors affecting plant development, especially bulbing and seedstalk formation, are included.

As indicated above, the literature on garlic is limited. Several recent works have dealt with onion anatomy, and most of the references on this subject may be found in Hoffman (1933),³ Hector (1938), and Hayward (1938). Other references dealing with the anatomy of the various species of *Allium*—in some cases specifically with garlic—which should be added to the above list include the papers by Irmisch (1850), Falkenberg (1876), Tavel (1887), Baldrati (1897), Menz (1910, 1922), and Braecke (1921).

General information on varieties of garlic and cultural problems is to be found in Beattie (1937), McCallum and Knott (1942), Comin (1942), Altstatt and Smith (1942), and Smith *et al.* (1944). About 80 per cent of the commercial garlic grown in the United States is produced in California (Rock, 1950). Here the crop is usually planted in fall or winter and begins growth with the fall rains. The plants grow slowly during the winter, more rapidly in the spring, and mature in June or July.

All observations reported here were made on either the Early or Late varieties of garlic as described by McCallum and Knott (1942). There are few qualitative anatomical differences between the two varieties, so that, except in special cases, no varietal designations will be given. It should be noted that varietal names in garlic have mostly only local application, and it is difficult to determine from the literature any varietal synonymy for the different garlic-growing areas in the United States.

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³ See "Literature Cited" for citations referred to in text by author and date.

The plant material from which slides, fresh sections, or cleared slices were prepared was almost entirely field-grown, using the common cultural procedures. Craf fixatives, usually III or V, were used (Sass, 1940) and prepared slides, except as noted, were stained in aqueous safranin followed by progressive Heidenhain's hematoxylin. Cleared slices (plate 3) were prepared by treating fresh sections with one or more changes of lactic acid (sp. gr. 1.20, 25° C).

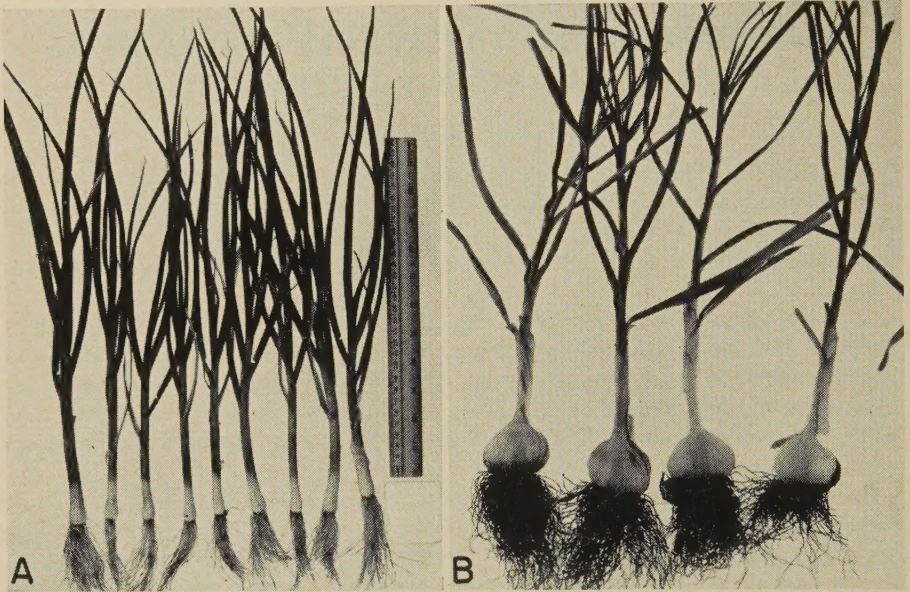


Fig. 1. Growth habit of garlic. A, immature Late garlic plants harvested in April. B, mature plants of Late garlic after harvest.

I. GROSS STRUCTURE OF THE GARLIC PLANT

Garlic under cultivation looks much like the common onion. Figure 1, A, shows immature garlic plants 3 to 4 months after planting, and B, mature garlic after harvest. The leaves, like those of the onion, are two-ranked and have sheathing bases. The two plants differ most obviously in the shape of the leaf blades and in the storage structures of the bulb. The leaf blades of the onion are round in cross section, and hollow; those of garlic are flat and slightly keeled as shown in figure 3, C. The outer layers of the mature garlic bulb are formed of the thin, dry sheathing bases of the foliage leaves as in the onion. If these dry sheaths are successively removed from the garlic bulb, a sheath is finally reached which not only surrounds the remainder of the bulb, but also bears in its axil a storage bud. Such a storage bud is commonly called a *clove*. This term is most frequently applied to the storage buds after they have been separated from the mother bulb. For this reason, the portion of the bud stem which remains with the mother bulb (plate 2, C and fig. 7, C) is not considered as part of the clove. The cloves themselves are actually small

bulbs, but to conform to well-established common terms, *bulb* will be applied only to the large, compound storage structure of the whole garlic plant.

One or more cloves will be found in the axil of each successive sheath progressing toward the center of the bulb. This is illustrated in plate 1, A, which shows parts of three bulbs from which several outer leaves and cloves have been removed. The groups of cloves shown here were each borne in the axil of a single leaf. In bulb 1, all central leaf bases and cloves have been removed to expose the stem. The bulb at A, 2 is shown in side view, and the one at A, 3 in top view. The latter shows clearly the more central cloves surrounded by the next thin, dry leaf sheath. In the onion, some of the leaf bases which correspond in position to these dry sheaths of garlic are fleshy and serve as food storage structures (Hoffman, 1933; Heath, 1945). Others are specialized for storage and lack functional blades, but they differ less from foliage leaves than do the leaves making up the cloves of garlic.

As the garlic plant matures, its main stem and all the foliage leaves and roots of the season's growth die and become dry; only the cloves, which abscise from the stem, remain alive. This annual pattern is followed whether the garlic flowers or produces vegetative growth only.

Arrangement of Bulb Parts

Details of the arrangement of cloves within the garlic bulb are shown in plate 2, A to D. A bulb cut crosswise through the middle is shown at A. Several leaf sheaths which surround the whole bulb are easily seen, but the bases of the foliage leaves which separate the groups of cloves are so thin that they are not visible in this photograph. The arrow across A shows the direction of the two ranks of leaf blades of this particular bulb. The cloves are produced in the leaf axil on the side of the bulb from which the leaf blade diverges. B is a diagram of the foliage leaf bases and cloves for the section shown at A. The sheathing bases of leaves which diverge to the right-hand side of the drawing are shown in solid lines, with the cloves axillary to these leaves outlined in heavy black. The opposite rank of leaves is shown by dotted lines, and the cloves are stippled. All cloves and leaves were removed from the bulb pictured at A, and the stem with projecting bases of lateral stems appeared as drawn at C. The projections where cloves were attached are numbered in the order of the grouping of the cloves from the outermost inward. All cloves common to a single foliage leaf received the same number. One small unnumbered projection had no visible clove. Diagram C is proportionately larger than A or B. The size of the stem relative to that of the whole bulb is shown at D, a longitudinal section. In a mature bulb, as shown here, the stem is so hard and dry that it is difficult to cut with a knife.

Six to eight sterile leaf sheaths, i.e., leaves that bear no cloves in their axils, are usually found on the outside of mature garlic bulbs. However, since these outer leaves are lost during growth and harvesting, a reliable figure for the total number must be based on counts started on young plants. Leaves of young plants were tagged in the field, counting the sheath-leaf immediately within the storage leaf of the clove as leaf number 1. It was found that there was an average of 13.6 and 11.8 sterile leaves surrounding the bulb in the Late and Early varieties respectively (Late, 8 bulbs, range 10-15 leaves; Early, 16 bulbs, range 10-14 leaves).

For leaves which bear cloves in their axils (fertile leaves), the number of cloves per leaf varies with the position of the leaf in the bulb. Data relating leaf position to number of cloves are shown for Late garlic at the left in figure 2. In this figure, leaf 1 for each bulb is the outermost leaf to bear a clove. Sterile leaves are usually not found between leaf 1 and any of the successive clove-bearing leaves. The outermost fertile leaf almost always bears

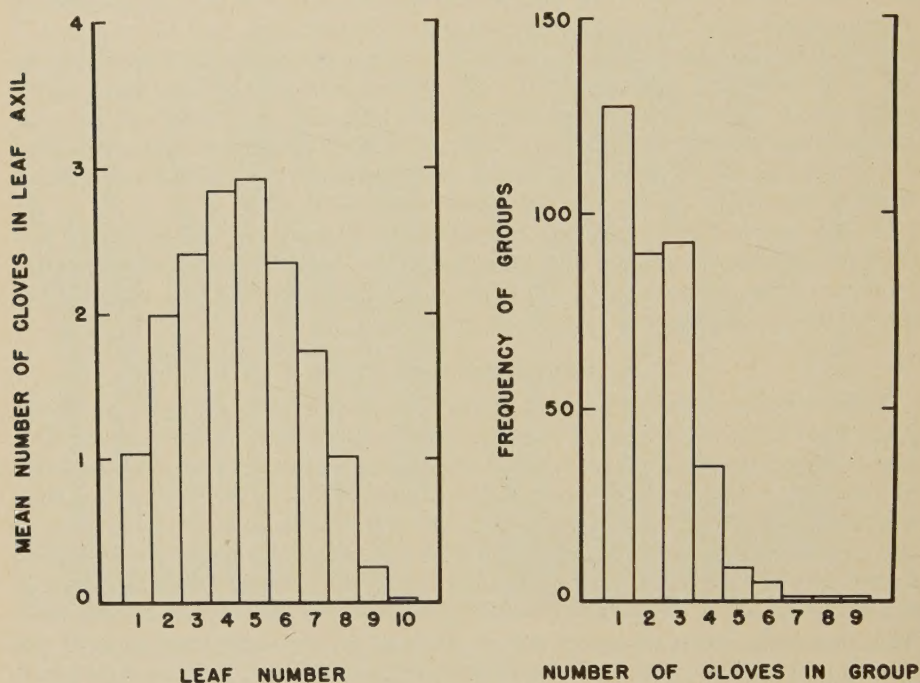


Fig. 2. Position of cloves in the garlic bulb. The figure on the left relates the number of cloves in the axil of a leaf to the position of the leaf in the bulb. For each bulb, leaf 1 is the outermost leaf to bear a clove in its axil, and the remaining leaves are numbered consecutively inward from this leaf. The figure on the right shows the frequency with which cloves in the leaf axils occurred in groups of 1 clove, 2 cloves, 3 cloves, etc. Both figures are based on 48 bulbs of Late garlic.

but one clove, and the number of cloves per leaf increases inward to the fourth or fifth leaf, where it averages about 3, and then decreases. While this graph shows the average number of cloves for specific leaves, it does not indicate how frequently the cloves in a single leaf axil are found in groups of 1, 2, 3, etc. The graph on the right of figure 2 summarizes this. Single cloves were most common; about half of the fertile leaves contained 2 or 3 cloves, and groups of 5 or more cloves were quite infrequent. The data in figure 2 were based on 48 bulbs of Late garlic. These averaged 16.7 cloves per bulb, and each bulb had about 7.5 clove-bearing leaves.

A typical garlic bulb may have, then, about a dozen outer sterile leaves—of which perhaps half are lost in growth and handling—and within these, 6 to 8 clove-bearing leaves with a total of 10 to 20 cloves.

Arrangement of Clove Parts

Plate 2, E, shows in cross section a single clove beneath which the leaves of a longitudinally split clove are separated and numbered consecutively from the outermost inward. Leaf 1, shown at the left, is here termed the *protective leaf* of the clove, since it has a tough lignified surface and in the practical handling of garlic protects the soft storage leaf which it surrounds. Leaf 2 constitutes the bulk of the clove, has a high content of stored food, and is termed the *storage leaf*. Leaf 3, here termed the *sprout leaf*, consists almost entirely of sheath, as is shown in figure 3, A and B. Braecke (1921) called this leaf the protective leaf since it surrounds the tips of the functional foliage

TABLE 1

WEIGHT DISTRIBUTION AMONG PARTS OF MATURE,
TRIMMED GARLIC BULBS FROM THREE SOURCES

Variety	Mean bulb weight,* grams	Weight of cloves as per cent of bulb weight	Storage leaf as per cent of clove weight
Late	14.0	95	82
Early	25.8	96	75
Late	49.2	95	80

* Mean of 5 average-sized bulbs.

leaves as they push up through the soil, but as mentioned above the term protective leaf is used here to refer to the outermost leaf of the clove. The fourth and fifth leaves shown are typical foliage leaves. In the photograph the fifth leaf surrounds four smaller foliage leaves, which were not separated out. The primordia of numerous adventitious roots cause the swollen area around the base of the stem. The dotted line in the figure is drawn through the junctions of the leaf blades and sheaths of leaves 4 and 5. The protective leaf may have a vestigial blade a few millimeters long, while the storage leaf consists of sheath only.

The weight distribution among the different parts of mature garlic bulbs is given in table 1. Figures are based on garlic from three different sources. The two samples of Late garlic were grown in different localities and had markedly different average bulb sizes. All bulbs were trimmed of roots and tops. The data on clove parts are based on 10 cloves of a size near average for each of the lots.

These data indicate that, even for widely different bulb sizes, the cloves constitute around 95 per cent of the bulb by weight, and the storage leaf around 80 per cent of the weight of the clove. Water loss during storage and also growth of the foliage leaves within the clove would affect these figures. These data were taken in late January, which is near the end of the storage period for the Early variety.

Several workers (Braecke, 1921; Belval, 1939; Kihara, 1939; and Anantakrishnan and Venkataraman, 1941) have studied the carbohydrate reserves in garlic or closely related species. The main carbohydrate appears to be a fructosan. Analysis in our laboratory indicates that the cloves, minus the

protective leaves, have around 40 per cent dry matter, by weight. This is very high; the common onion varieties range between 8 and 16 per cent dry weight.

The arrangement of parts of a garlic clove is readily seen when it begins to sprout. Such a clove taken from the field a few weeks after planting is shown in figure 3, A. The protective leaf, P, still surrounds the clove, and from the

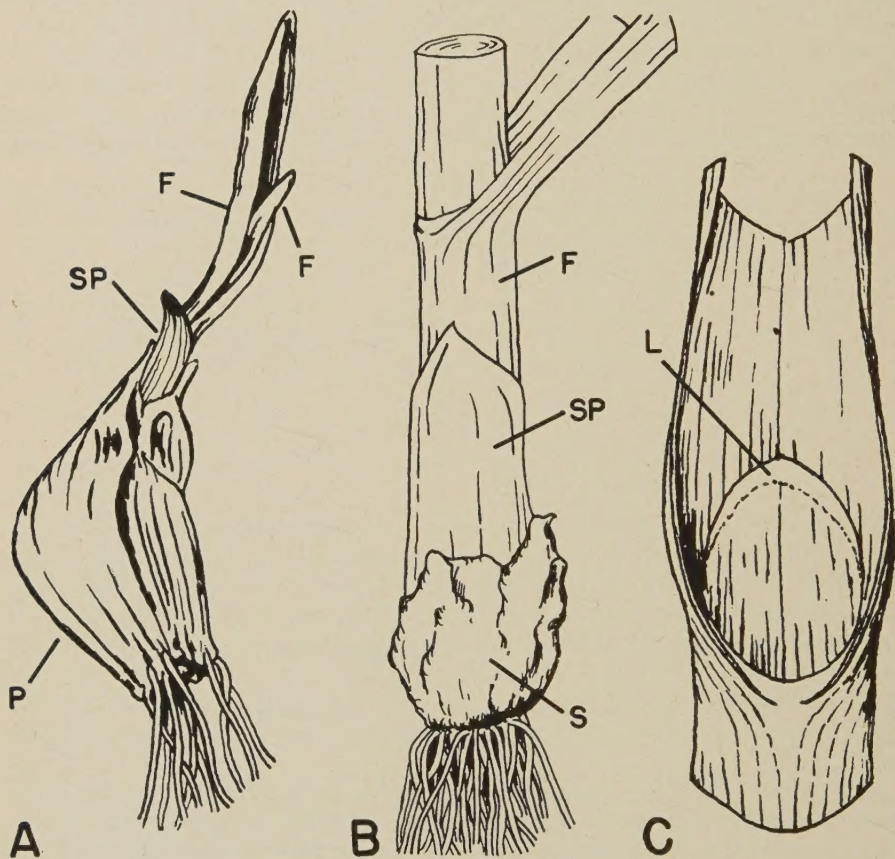


Fig. 3. A, a sprouting garlic clove still surrounded by the protective leaf, P. From the clove tip protrude the sprout leaf, Sp, and the elongating blades of foliage leaves, F. B, a young plant with a depleted storage leaf S, sprout leaf Sp, and the first foliage leaf, F. C, a portion of a foliage leaf showing the shape of the leaf blade and the ligule, L.

stem protrude numerous adventitious roots. Many of these roots, which are produced abundantly and quickly when mature, nondormant cloves are planted in moist soil, are initiated while the clove is still growing on the mother bulb; an average mature clove possesses 20-40 well-developed but unelongated roots (plate 2, E, 5; fig. 7, B). Even before planting, some of these penetrate completely through the thick base of the storage leaf, but most of them are still embedded. Usually the cloves of a bulb, except those near the center, are quite asymmetrical, and most of the roots develop on the

lower side. This may be seen in the cleared sections, plate 5, A (longitudinal) and B (cross). As described below under stem structure, new roots continue to be initiated as the plant grows.

The shape and extent of the root system of field-grown garlic has been described by Weaver and Bruner (1927), who found that mature plants possessed 40-60 roots, which spread laterally some 18 inches and downward about 2½ feet. They pointed out that this system resembles closely that of onion and leek.

Returning to figure 3, A, one will note the two elongating foliage leaves, F, and below these, at Sp, the sprout leaf. Figure 3, B, shows the base of a plant slightly younger than that shown in figure 1, A. The top with several expanded foliage leaves has been removed, leaving the sheath and part of the blade of the foliage leaf, F; the sprout leaf, Sp; and the storage leaf, S, which is mostly depleted of food and partly decayed. At C is a portion of a foliage leaf showing the ligule, L, and the shape of the blade.

Seedstalks, Top-sets, and Seeds

Seedstalks in garlic develop from the tip of the main stem, terminating further vegetative growth. In no cases observed have lateral buds continued vegetative growth, as occurs in the onion (Heath, 1945). Seedstalks in garlic, insofar as the author has observed, always bear a cluster of small bulbs in the inflorescence. This agrees with the observations of Weber (1929), and other authors have used the presence of bulbs in the inflorescence to distinguish garlic from several of the flat-leaved alliums such as Great Headed or Spanish Garlic, *A. ampeloprasum* L., and Leek, *A. porrum* L. (Krause, 1930; Bailey, 1949).

Flowers are usually mixed among the top-sets, though at times they may be small and inconspicuous (Weber, 1929). The flowers are apparently sterile. This has been reported by Kirchner *et al.* (1912), Weber (1929), Jones (1937), and Krivenko (1938). There are many references to the true seed of garlic in the literature, but since no author who speaks of garlic seed states that viable seed has been seen first-hand (however, see Stephenson and Churchill, 1835), it seems most probable that true seed of garlic is not known.

Plants producing seedstalks also produce a bulb with cloves at the ground level. Seeders are commercially undesirable, however, because of reduced yields and because of the hard seedstalk through the bulb center. A short seedstalk bearing a cluster of top-sets close to the top of the main bulb as observed by Debbarman (1923) is not uncommon.

Abnormalities of Bulb Development

The foregoing description of the garlic bulb is based on averages; it is a picture of an ideal rather than a typical bulb, and does not reveal the variability in form and arrangement frequently encountered. Wide differences occur, of course, among the many varieties of garlic (Jones, 1937); but apart from this, morphological variation within the usually grown kinds may be considerable.

Examination of bulbs over several seasons makes it clear that cloves may

appear, on occasion, in almost any leaf, or that the protective or storage leaves may produce elongate green blades, or may be anomalous in number or position. These variations are so frequent that it is, indeed, almost an unusual bulb that follows in all details the pattern outlined above.

The value of a commercial crop may be lowered by deviation from the above growth pattern—for example, “doubles,” i.e., the development of two bulbs from a single clove. Examination of planting stocks which produce frequent doubles indicates that these arise from cloves containing two storage leaves and growing points within a single protective leaf. Some of these double cloves have perfectly smooth exteriors and can hardly be discarded by grading.

On the other hand, doubles or extremely rough bulbs may result from initiation of buds very near the bulb exterior, i.e., in the axils of leaves which are usually sterile. For example, one particular lot of 114 cloves which was dissected showed that 15 per cent of the cloves contained tiny buds in the fifth to seventh leaf axils. The cause of this unusual deviation is not known, but it is evident that garlic grown from these cloves would be unusually rough.

Doubles are mentioned only as an example; there are other morphological defects occurring frequently enough to have received common names (Beattie, 1937; Altstatt and Smith, 1942). In general, nothing is known of their cause at the present time, but they are important since they lower the grade of commercial garlic.

Gross Structure of Garlic Compared to that of Other *Allium* Species

In the above description, the structure of the garlic plant was compared with that of the onion, because the growth pattern of the latter is fairly well known. A comparison of its structure with that of other *Allium* species is of interest, especially since onion and garlic are in so many ways dissimilar. However, apart from recent work on *Allium cepa* L., and excepting anatomical details for several species, there appears to have been no study on gross development of any of the *Alliums* since the paper of Thilo Irmisch in 1850.

Irmisch studied seasonal development in about 12 species, among which were *Allium sativum* L., *A. cepa* L., *A. fistulosum* L., *A. porrum* L., and *A. schoenoprasum* L. Unfortunately, he devoted little space to the above species, since he felt that the growth patterns of cultivated forms were so variable, because of their cultural treatments, that there was little that was safe to observe. His data on garlic and onion, though brief, are correct.

Among uncultivated forms, Irmisch investigated several whose development is much closer to garlic than to onion. These include *Allium vineale* L. (see also Iltis, 1949), *A. scorodoprasum* L., *A. rotundum* L., and *A. moly* L. In each of these, the bulb goes through a dormant period in which a single leaf sheath serves as a food storage organ. This storage leaf may be unprotected, but is usually surrounded by one or two protective leaves. The first leaf produced when active growth begins is a sheath leaf with a much reduced blade (sprout leaf). This is followed by two to several foliage leaves. In all the uncultivated species listed above, small bulbs (cloves) are formed

in axils of the foliage leaves. The shoot apex produces a terminal flower stalk, and in the axil of the last foliage leaf (at the base of the flower stalk) the main bulb is formed. This main bulb, to which is attached more or less of the stem from the previous year, continues the perennial growth of the plant. The small side bulbs may form separate plants.

The growth pattern of garlic is very similar to the growth patterns just described, especially if one assumes that no main bulb is formed. Many more foliage leaves develop in garlic than in the species described by Irmisch (*Allium scorodoprasum* L., with 5 to 7 leaves, had the most), and all of the reserve food goes into the small bulbs serving for vegetative multiplication. This modification in garlic appears to be in the opposite direction from that in *A. ursinum* L. which, as Irmisch showed, forms no cloves—only a main bulb—so that vegetative multiplication does not occur.

II. BULB DEVELOPMENT IN FIELD-GROWN GARLIC^{*}

The development of garlic plants in the field was studied by measuring plant size, bulb enlargement, and differentiation of leaves and cloves of Early and Late garlic at intervals during the growing season.

Early garlic was planted in the field at Davis on November 8, 1941, and harvested in mid-July, 1942. Samples were measured and dissected on the dates indicated on the upper graph in figure 4. The garlic was from two sources: Chualar, California; and Walla Walla, Washington. Bulbs from both sources were divided into two lots and stored at 32° and 50° F from August 21, 1941, until planting. The data in figure 4 are means of samples of 10 to 30 plants from each of four lots (2 sources \times 2 storage temperatures). While there were some significant effects of source and of storage temperature, the differences were small and the means are used here since they give perhaps the most satisfactory general picture.

Late garlic was field-planted December 5, 1941, and harvested July 17–18, 1942. Bulbs were sampled on the dates indicated on the lower graph in figure 4. This garlic consisted of two lots, both originally from Oregon, but grown in California one and two years. Storage time and temperatures were the same as for the Early variety. Data in figure 4 are means of samples of 10 bulbs from each of the 4 treatments (2 sources \times 2 storage temperatures).

Mean plant height (length of longest leaf, base to tip) increased for both varieties until mid- or late May.

In recording the total number of leaves, the storage leaf was counted as the oldest leaf, and leaves down to the smallest primordium visible under the dissecting microscope were included. The number of leaves increased throughout May for the Late variety, and apparently into early May for the Early variety. Later in the spring, when the outer leaves became dry and partly decayed, total leaf counts could not be made. However, a good estimate of total leaves was made from the position of the outermost cloves. These estimates are shown as dotted extensions of total leaf number curves. For both varieties, the total number of leaves formed probably lies between

^{*} Several of the early experiments on bulb development in field-grown garlic were initiated by Dr. J. E. Knott.

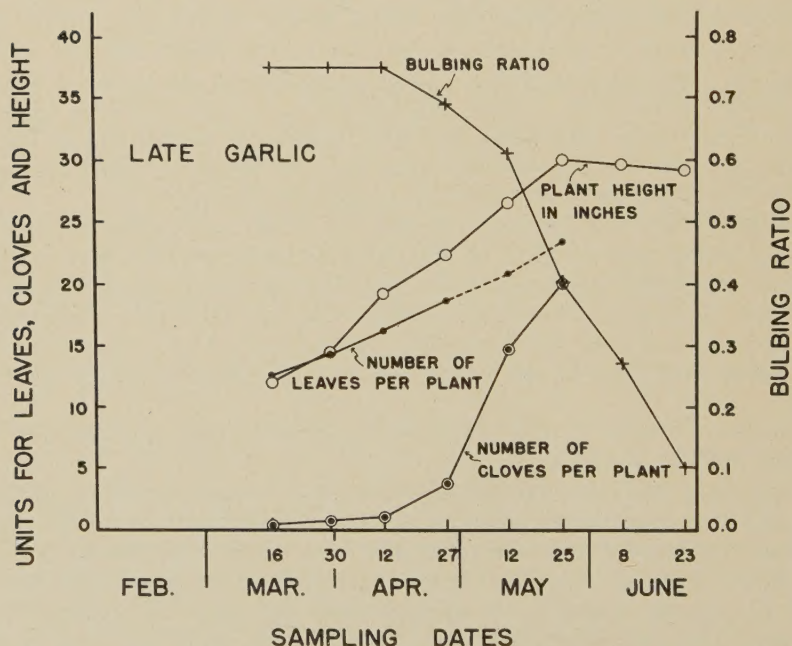
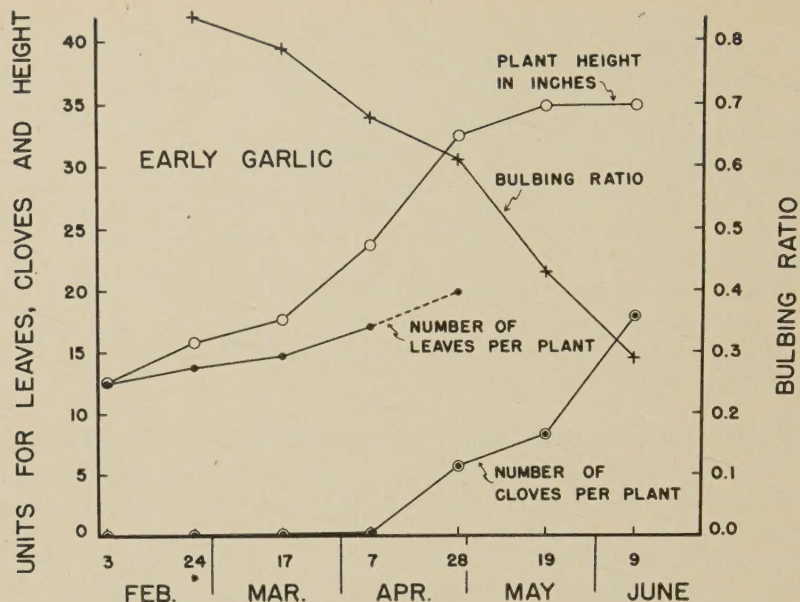


Fig. 4. Development of Early and Late garlic in field plots, planted at Davis, Calif. on November 8 and December 5, respectively. The plant height is the length, from base to tip, of the longest leaf. The bulbing ratio is the diameter of the neck divided by the bulb diameter. When values of this ratio drop below about 0.5, the plant appears to have a definite bulb. Most points on the graph are means from 40 plants. The dotted lines connected estimated values.

20 and 25. The last leaves to form are initiated after bulbing is well started, and there is little opportunity for their development.

The number of leaves visible without dissection, i.e., as plants are seen in the field, was also recorded, but is not shown on the graphs. This number increased from about 5 leaves on the earliest sampling date for each variety to about 10 for both varieties in early April, and remained at this level. Loss of outer leaves and slow development of inner ones account for the small number of visible leaves.

For both varieties, cloves began differentiating in mid- to late April and increased in number rapidly in May. The last dissections showed about 20 cloves per bulb. Mature bulbs seldom contain more well-developed cloves than this; thus the cloves which constitute the main portion of the bulb have all appeared by late May or early June.

The swelling of the bulb is represented on the graph by the ratio—neck diameter/bulb diameter. This ratio appears to indicate bulbing quite well and is independent of plant size or units used. Any ratio below 0.50 indicates a definite bulb, and ratios of 0.20 to 0.15 usually indicate maturing bulbs. Bulbing parallels clove differentiation very closely. The early decrease of the bulbing ratio is partly from swelling of the foliage leaf bases, but clove growth is rapid and almost all the bulb growth may be attributed to this. Thus, for Late garlic on May 29, when the bulbing ratio was 0.4, a random sample of 10 bulbs showed that each bulb had an average of 1.6 cloves with only 1 differentiated leaf, 2.8 cloves with 2 leaves, 3.9 cloves with 3, 5.5 with 4, 3.8 with 5, and 0.7 with 6. Data of this type were taken over the whole season, and they indicate that cloves increase rapidly in size after they first appear. Cloves in outer leaf axils may be quite large and contain several leaves while cloves near the center of the bulb are still being differentiated. It is for this reason that the early period of bulb enlargement is simultaneous with rapid clove initiation.

After plants have been harvested, additional leaf initials may form in the cloves during storage. An example may be taken from the same lots of Late garlic as were described above, which had been placed at 32° and 50° F storage on August 21. A lot of 172 cloves from 32° F was dissected on January 17–20 and showed an average of 7.35 (range 6–9) leaves within the storage leaf, while 197 cloves from the 50° F storage had an average of 8.32 (range 7–11) leaves. The leaves within the storage leaf also increase in length (sprouting), a change which is much more conspicuous than the initiation of new leaves.

III. FACTORS DETERMINING BULBING AND SEEDSTALK FORMATION IN GARLIC

Bulb Formation

The description of garlic presented in this paper is concerned primarily with the garlic bulb. As no data on bulbing of garlic have been published, a brief summary of experiments indicating the environmental factors affecting bulb formation is given here.

To determine the effect of day length on bulbing, pots containing sprouted

TABLE 2

MATURITY AND BULBING OF EARLY AND LATE GARLIC GROWN UNDER LONG AND SHORT DAYS AT TWO TEMPERATURES. LONG-DAY BENCHES LIGHTED FROM 6 TO 10 P.M.; SHORT-DAY BENCHES COVERED FROM 6 P.M. TO 10 A.M. CLOVES PLANTED FEBRUARY 20

	Greenhouse Day 60° F, night 50° F				Greenhouse Day 50° F, night 40° F			
	Long day		Short day		Long day		Short day	
	Condition of tops	Neck diameter* Bulb diameter	Condition of tops	Neck diameter* Bulb diameter	Condition of tops	Neck diameter* Bulb diameter	Condition of tops	Neck diameter* Bulb diameter
Early garlic								
5/4.....	Down, partly mature	0.19	Up, green	0.38	Up, green	0.28	Up, green	0.43
5/27.....	Mature (harvested)	0.10	Down, green to part dry	0.23	Down, green to dry	0.14	Up, green	0.28
6/17.....	Mature	<0.22	Mature	0.16	Mostly mature	<0.18
Late garlic								
5/4.....	Up, green	0.35	Up, green	0.57	Up, green	0.44	Up, green	0.60
5/27.....	Down, green	0.27	Up, green	0.53	Up, green	0.28	Up, green	0.54
6/17.....	Mature	<0.17	Down, mostly green	<0.38	Down, mostly dry	0.17	Up, green	0.53

* Values below about 0.50 indicate definite bulbs.

cloves of Late garlic were placed under 18- and 11-hour days, 10 plants under each. The plantings, made in late January, were in a greenhouse kept near 70° F day and night. Two months later, the plants under long days were bulbing, but those under short days were not. When the plants under long days were nearly mature and the tops were drying, those under short days were green and showed no evidence of bulbing.

In another test, the Early and Late varieties were each grown on two day lengths in two greenhouses, one held at 40–50° F (40° night, 50° day) and

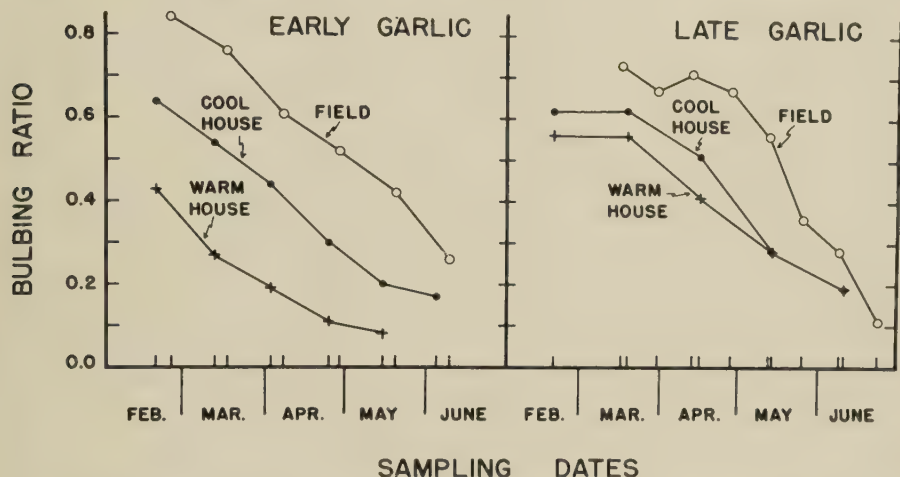


Fig. 5. Bulbing of early and late garlic grown in the field at Davis, Calif., and in a cool (40° F night, 50° F day) and warm (50° F night, 60° F day) greenhouse, all under natural daylength. The bulbs were stored at 32° F from August 21 until planting and planted in the field November 8 (Early variety) and December 5 (Late variety), and in the greenhouses November 3 (Early and Late).

the other at 50–60° F (50° night, 60° day). The long-day lots were lighted from 6 p.m. until 10 p.m.; the short-day lots were covered with black cloth from 6 p.m. until 10 a.m. the following day. The cloves were planted in flats on February 20. Each lot had 18 cloves, though in the Early variety roughly half of these failed to germinate so that these lots were small. Data from this test are given in table 2. The degree of bulbing is indicated by the ratio of neck diameter to bulb diameter as described above. These data indicate that, within the limits of the day lengths and temperatures used, long days and high temperatures favor bulbing. Bulbing in Late garlic, as compared to Early, appears to be delayed by both short days and low temperatures.

The growth of Early and Late garlic in the field has been discussed (fig. 4). Some of the same garlic used for the tests shown in figure 4 was grown under natural day lengths in the 40–50° F and 50–60° F greenhouses. The cloves of both varieties had been stored at 32° F since August 21. The lots were planted in the greenhouse on November 21, 13 days after the Early variety was planted in the field and 15 days before the Late was planted.

Bulbing data for these lots of garlic grown in the two greenhouses and in the field are shown in figure 5.

The differences in bulbing among the lots of Early garlic (fig. 5) must be attributed almost entirely to temperature. The earlier planting of the field lots would tend to decrease the observed differences, but it is doubtful if this effect would be large, especially late in the season.

For the Late garlic, bulbing began more quickly in the warm than in the cool house, but the differences disappeared as the plants matured. The lot grown in the field was the slowest to start bulbing. However, considering that it was planted 15 days later than the plants grown in the greenhouse, the difference in bulbing ratio as the plants began to mature was quite small.

On the basis of the above tests, it would seem that the bulbing of commercial garlic occurs in the spring in response to lengthening days and increasing temperatures. Plantings in southern areas may bulb earliest because of higher temperatures, in spite of the longer days in areas farther north. Since bulbing of Early garlic seems more responsive to temperature than the bulbing of Late garlic, warm weather late in the spring may have more effect on its maturing. The control of bulbing in garlic by day length and temperature appears to be quite like that in onion (Magruder *et al.*, 1941). However, we do need more data on the critical day lengths of the two garlic varieties and their relation to temperature. Varietal differences in earliness could also depend in part on rate of development after conditions have become favorable for bulb initiation.

Bulbing in garlic may also be affected by the storage temperature of the bulbs prior to planting, as is shown in the following experiment. Bulbs of five clonal lines of Early garlic were placed in storage on October 1 at the following temperatures: 32° F (range 31–34°), 40° F (range 38–44°), 50° F (range 50–52°), and 60° F (held essentially constant). The bulbs were removed December 18, and 30 to 60 cloves of each clone were planted in the field. Approximately one-third of all cloves had sprouted (emergence of foliage leaves through storage leaf) at all storage temperatures except 32°, where there was practically no sprouting. In addition to the field planting, five cloves from each temperature were planted in the 40–50° F greenhouse and also in the 50–60° F greenhouse.

By May 3 the plants from cloves stored at 32° and planted in the 50–60° house were mature. On this same date, the 40° bulbs were nearly mature, the 50° bulbs had partly dry tops, but the 60° bulbs were upright and green and showed little evidence of bulbing. By May 27 the 50° storage lot was mostly mature, and by June 18, though the tops of the 60° lot were still up, they were drying and the bulbs were fairly well formed.

Plants grown in the 40–50° F greenhouse likewise showed earliest maturity from cloves which had been stored at low temperatures, though development in all lots was slower than in the 50–60° house.

The field-grown plants showed much less effect of storage temperature than did the plants grown in the greenhouses. In fact, only the 60° F storage lot was distinguishable in top growth. Bulb and neck measurements made May 27 on one clonal line (10 bulbs from each storage temperature) disclosed no significant effect of storage temperature on bulbing.

In the field tests on which figures 4 and 5 are based, the Early and Late varieties had been stored at both 32° and 50° F before planting. The bulbing data (neck diameter/bulb diameter) for the two storage temperatures show that, for both varieties, the plants from cloves stored at 32° began to bulb most quickly. However, by May 19 for the Early garlic, and by June 8 for the Late, the differences in bulbing were no longer evident.

In another field test, differences in earliness resulting from storage temperatures persisted until harvest. Late garlic was stored at 32° F, 50° F, and in an open shed (near Hollister, California) and was planted in the field on January 13. The plants from bulbs stored at 32° F grew most rapidly and matured about one week before those from bulbs stored at 50° F. The shed-storage bulbs produced plants which matured a few days later than the 50° F storage plants.

The greenhouse plantings described above show that clove storage temperature may have a definite effect on subsequent bulb formation. It is not surprising, however, that the effect of low-temperature storage on field plantings was always slight, since these plantings were subjected to from 2 to 3 months' low temperature in the field before conditions of temperature and day length became favorable for the initiation of bulbs.

Heath *et al.* (1947) reported that the maturity of onion plants grown in the field from sets was delayed if the sets had been stored at high temperatures. Their report indicated that, for 14 weeks' storage, 68° F delays ripening as much as higher temperatures, but that there was little difference in maturity between sets stored at 32° and 45° F. The data on garlic suggest that differences between the 32° and 45° storage of the onions might have been evident had they been grown in greenhouses at higher temperatures.

Storage temperature has an additional and perhaps quite separate influence on garlic growth in that it affects clove dormancy. Freshly harvested garlic will not sprout readily if field-planted and irrigated. Experiments now in progress indicate that storage temperatures have a marked effect on this dormancy. What relation there may be between the effect of storage temperature on dormancy and its effect on time of bulbing and maturity is not yet known.

Seedstalk Formation

The physiology of bolting in garlic is not understood. In some years, the commercial fields in California may have a high proportion of bolters; in other years bolters may be difficult to find. Much of the garlic imported from Mexico and South America has seedstalks in all bulbs.

In 1944 plants with seedstalks were collected in the Salinas and San Juan areas in California. Progeny from these plants grown at Davis produced no seedstalks. While seedstalks are observed more frequently in the Late than in the Early variety, and while Altstatt and Smith (1942) observed that several strains grown in Texas differed in their tendency to bolt, there is no evidence that seeders in commercial fields are a distinct strain mixed in with other planting stock (a belief common among growers).

Since bolting in the onion is induced by exposing bulbs or growing plants of a minimum size to low temperatures, such treatments were tried on garlic. The experiments described above, in which cloves were stored at various

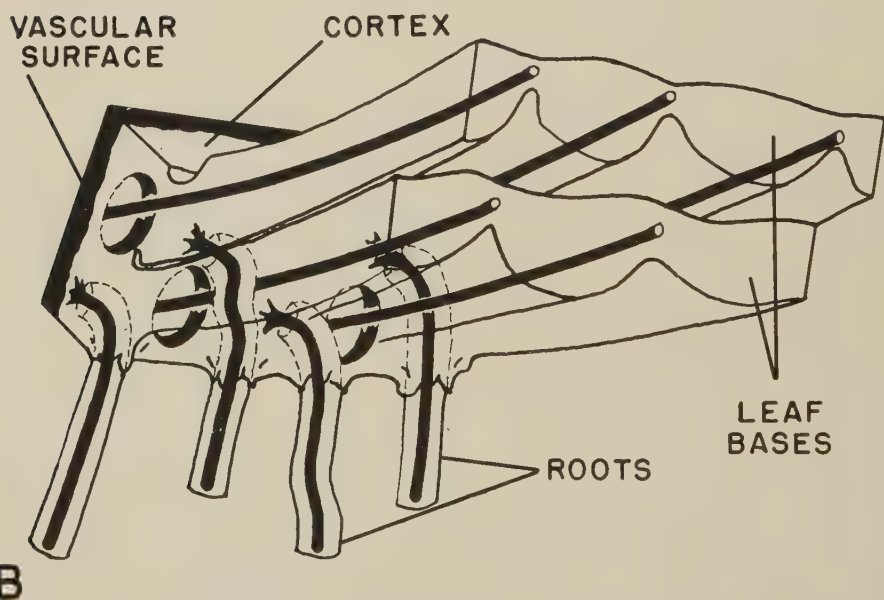
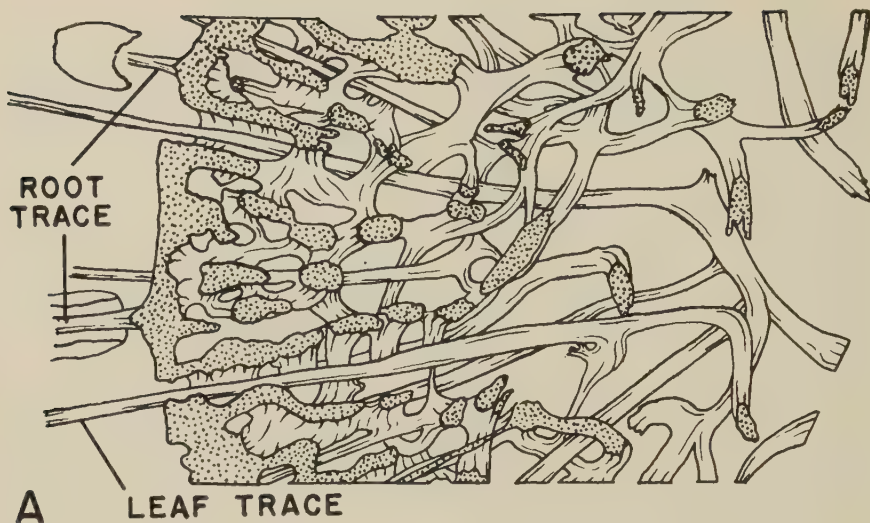


Fig. 6. A, a drawing showing details of the area outlined in the photograph, plate 3, A. B, a diagrammatic drawing of vascular connections of the roots and leaves to the stem. The solid black portion of the stem represents the surface of the vascular network. The traces of the leaves pass through this layer; the root traces attach to its surface.

temperatures before planting, were attempts to induce seeding. No bolting occurred in any of the treatments tried.

In another attempt to induce bolting, growing plants were subjected to low night temperatures. Several flats of both Early and Late garlic were

planted outside at Davis on December 20. On January 6, after they were well sprouted, two flats of each variety were placed in a 32° F room, a 40° F room, and a 50–60° F greenhouse. The flats from the temperature-control rooms were placed outside each morning between 8:00 and 8:30, and replaced in the specified temperature at sunset. The Early garlic was given 2 weeks and 4 weeks at each of the temperatures, and the Late garlic 2 weeks and 8 weeks. After the temperature treatments were finished, all flats remained outside until the plants were mature. No differences among treatments were evident, and seedstalks did not form.

In experiments on bolting, the effect of temperature, either during storage or later, would be most evident on plots in which approximately half of the plants bolted. While the above experiments demonstrate that plants can be subjected to considerable chilling without bolting, the effect of temperature on bolting is difficult to evaluate since bolters were absent from all lots.

The only report in the literature on the physiology of bolting is that of Vanin (1947), who stated that cloves grown under poor cultural conditions (drought, weeds, crowding) give rise to bulbs containing but one clove, and that these produce seedstalks the following year. Vanin also stated that small top-sets react as do ordinary cloves, but large top-sets may give seedstalks directly. He added that, once induced, seedstalk production is heritable. We have observed that single-clove bulbs form under poor cultural conditions, but have not checked these for seedstalk production. The single, symmetrical cloves which Vanin described are rarely present in seed used for commercial production, in which bolting is sometimes a problem.

IV. STRUCTURE OF THE STEM

Except when a seedstalk is formed, the internodes of the garlic stem are short, each leaf base being in contact with the leaf bases immediately above and below. During most of the growing season, the stem is roughly hemispherical with the flat side uppermost (plate 1, B). This upper surface which bears the cloves may become convex at maturity, the whole stem being slightly broader than long (plate 2, D). In cross section, the stem is round (plate 3, A) except in the early stages of growth (plate 5, B).

The gross arrangement of vascular tissue in the stem is easily seen in cleared slices (plate 1, B and C; plate 3, A). The central cylinder of the stem is a complex network of vascular bundles, rather open near the stem apex, but quite dense near its well-defined lateral surface, and with fewer strands in the center. This cylinder has roughly the same shape as the stem and is surrounded by a thick cortex. The latter is devoid of vascular tissue except for the leaf and root traces which cross it almost at right angles. Except in quite young garlic bulbs, there is no region in the central cylinder sufficiently free of vascular tissue to be termed pith, though this tissue may be well delimited in onion bulbs (Hoffman, 1933, fig. 2; Heath, 1945, fig. 2).

The Course of Leaf Traces in the Stem

The vascular bundles of the leaves follow a path from the leaf base directly across the cortex and into the central cylinder, entering the latter almost at right angles to its surface (plate 1, C). Within the central cylinder

the traces follow a slightly downward course toward the stem center until they connect to other vascular bundles. A cleared, transverse slice of stem parallel to these traces in the central cylinder is shown in plate 3, A, with a portion redrawn as figure 6, A, to give greater detail. The leaf traces do not connect with other vascular tissue in passing through the rather dense surface of the vascular cylinder. A section tangential to this surface shows the traces end-on, each surrounded by parenchyma (central part of plate 3, B). The strands to which the traces first connect anastomose with still other bundles to become part of the large net-like vascular cylinder. The largest leaf traces penetrate most deeply, but even the smallest penetrate some distance into the central cylinder before anastomosing. As anastomosis takes place, it becomes more and more difficult to determine the course of any individual leaf trace. However, the turning back toward the stem periphery, of at least the larger traces, is evident in the stem center (fig. 6, A). In the onion stem, it is in this region that the leaf traces describe circular paths delimiting the pith area. These bundles surrounding the pith form what Hoffman (1933) termed the "perimedullary vascular cylinder"; this arrangement of bundles is usually not evident in garlic.

The vascular pattern in the garlic stem follows the *palm type* or Falkenberg's type II. Falkenberg (1876) placed *Allium cepa* L. in this group, and considered it a good example among bulb plants because of the relatively few anastomoses of the leaf traces in the stem. In a stem with the palm type of vascularization, those leaf traces which penetrate toward the stem center return again to the surface of the vascular cylinder. Because of anastomosis, however, this ideal pattern can seldom be clearly followed; in garlic, the sparse vascular network in the central portion of the stem, the leaf traces leading directly to this central region, and the dense, much branched outer vascular layers conform well to the palm type.

Falkenberg (1876) pointed out that forms like *Allium*, which lack long internodes, show the palm type of vascularization much more clearly than plants like *Zea* and *Saccharum*, where leaf traces are difficult to follow because the nodal regions become widely separated by intercalary growth. On the other hand, where internodes are short, as in garlic, it is difficult to distinguish nodal regions in the central cylinder. Structures which appear to be nodal regions can be seen in plate 1, C. Here the leaf traces, in passing to the center of the vascular cylinder, cross several fairly definite networks that arch upward toward the stem center, i.e., are dome-shaped. These roughly horizontal networks can usually be distinguished, and it seems possible that they are nodal structures, i.e., correspond to the nodal plates of *Zea*. The larger leaf traces cross several of these before reaching the stem center, which would imply that they pass downward through several nodes. Krauss (1948) stated that in the pineapple stem, which is similarly congested, there is no evidence of an orientation of bundles into nodal and internodal regions in the central cylinder.

The structure of the leaf traces, as they approach the center of the vascular cylinder, is modified from the form in the leaf in two respects. First, the xylem and phloem change from a collateral to an amphivasal arrangement, a condition apparently common to many monocotyledons

(Cheadle and Uhl, 1948; Haberlandt, 1914). Second, as the traces approach the center of the vascular cylinder they no longer show a well-defined protoxylem; the first xylem to mature differentiates with scalariform thickenings. This type of xylem characterizes the whole vascular cylinder except the incoming leaf traces, where the first xylem matures across the still-growing stem apex (plate 6, A) and is later destroyed by growth changes.

Connections of Root Traces in the Stem

The root traces connect to the outer surface of the vascular cylinder, which, except for the openings through which the leaf traces pass, presents an almost continuous layer of vascular tissue. The root traces do not penetrate, as distinct bundles, into any part of the stem vascular network (plate 1, B and C; plate 3, A and B; plate 5, A; fig. 6, A).

Figure 6, B, representing a stem surface and two attached leaf bases, shows in a diagrammatic fashion the penetration of the leaf traces through the surface of the vascular structure of the stem, and the connection of the root traces to its surface. Parts of four adventitious roots, and five traces in two sheathing leaves are shown.

Traces of Lateral Buds (Cloves)

The developing cloves are located on the upper surface of the stem (plate 1, B). The small network of vascular tissue at the base of each clove is connected to the network of the main stem by a number of traces. These traces, which are not individual leaf traces but come from the much-branched vascular cylinder of the clove, join with the upper surface of the stem network of the bulb. Here the network is quite open, lacking the well-defined surface present on the sides of the stem. Thus the clove traces all penetrate into the central cylinder, but much less deeply than do the larger leaf traces. Because of the lack of internodes, it is difficult to determine if the clove traces, in their union with the main stem, follow any pattern, such as one of the several which Falkenberg (1876) described for the monocotyledons.

Structure of the Clove Stem

Some features peculiar to the clove stem were not covered in the above discussion and will be mentioned here.

The vascular system of the young clove is shown diagrammatically in figure 7, A, and in a cleared, longitudinal section in plate 4. From these pictures, it can be seen that the vascular strands of the protective leaf enter the clove stem near its base, well below the region where the outer strands of the storage leaf bend inward. As the clove grows, the main vascular network of the stem develops in the region where the outer strands of the storage leaf converge. Thus, between the point of convergence of the outer traces of the storage leaf and the traces of the protective leaf, there is a relatively long stem region with no connecting leaf traces. The thickened base of the storage leaf fills this area so that no internode is evident on the stem surface. As the clove matures, adventitious roots develop near the

base of the storage leaf, and this region becomes swollen (plate 2, E, 5). This swelling causes a loosening of the lower edge of the storage leaf from its stem. The protective leaf abscises completely so that immediately beneath the storage leaf there is a region of bare stem several millimeters long (fig. 7, B). An abscission layer develops across this region and separates the clove from the mother bulb as shown in figure 7, C. The cloves as they separate from the bulb carry the dry, dead protective leaf, but leave behind short lengths of stem which bear the node from which the protective

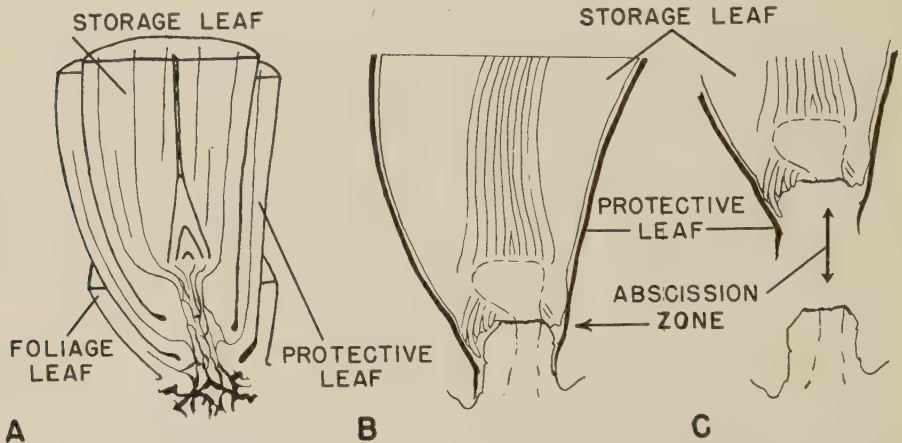


Fig. 7. A, the leaves and vascular connections of an immature garlic clove. B and C, abscission of a mature garlic clove. The abscission zone crosses the stem of the bud between the nodes of the protective leaf and the storage leaf. The protective leaf remains with the storage leaf which it closely surrounds. The stems below the abscission zone are left as projections on the stem of the mother bulb (plate 2, C), and do not constitute a part of the clove.

leaf has abscised. These are the projections shown in plate 2, C, and like other parts of the mature bulb they become partly lignified and dry.

The vascular tissues of a mature clove are shown in the photographs of cleared sections in plate 5. The protective leaf, which has no direct connection to the clove stem (fig. 7), has been removed. In the longitudinal section at A is seen the abscission layer and the storage leaf surrounding the developing foliage leaves. This section was cut radially with respect to the mother bulb. In the picture the adaxial side (again with respect to the mother bulb) lies to the left. It can be seen that the vascular structures are quite asymmetrical. This varies with the position of the clove in the bulb; cloves near the apex of the bulb are mostly symmetrical, but those borne on the side of the bulb are less so. In the asymmetrical cloves, the earliest adventitious roots are all on the abaxial side. Also in these cloves the vascular surface, with which the root traces connect, is more prominent on the abaxial side, and appears before the traces. This layer is very well defined, even though the bundles making up the vascular network are rather scattered. Between the vascular network and the abscission layer are the traces, usually about 20, which connected the clove to the bulb.

The Cortex, the Central Cylinder, and Associated Tissues

The development of primary tissues in monocotyledonous stems has been reviewed by Esau (1943) and Krauss (1948). The only study of stem development in any species of *Allium* appears to be Falkenberg's work (1876) on the onion. His observations on the development of the cortex and central cylinder, though brief, are similar to those outlined below for garlic. Mangin (1882) mentioned *Allium cepa* L. among examples of stem types found in annual, scaly-bulbed plants, but gave no details; and Hoffman (1933) confined his description of the stem apex to the seedling.

The following brief picture of the garlic stem is mainly descriptive—no detailed studies on tissue origins and relationships have been made.

In garlic, the stem regions usually termed cortex and central cylinder are clearly defined (plate 6, A), and in fresh stems are easily distinguished by the naked eye. The marked differences in the amount of vascular tissue in the central cylinder and the cortex have been described, and additional differences in texture are evident at low magnifications. The distinction between these two regions is lost, however, at the stem tip. Beneath the stem apex and the bases of the first two or three leaves surrounding the apex is a region of rather uniform parenchyma and conspicuous procambial strands. Among these are traces connecting directly to the young leaves and other traces running parallel to the stem surface. These latter, when mature, will form part of the vascular tissue of the central cylinder. Although this region contains dividing cells, it shows no distinctly oriented meristematic activity.

The parenchyma beneath the leaf bases farther from the stem tip—beyond about the third leaf—divides repeatedly, almost altogether periclinally, so that the cells of this region, as one follows it away from the stem tip, appear in conspicuous radial files (plate 6, B). This oriented cell division occurs in the whole upper portion of the stem. Cells divide over a wide region, so that no particular row of cells can be designated as a center of activity. In the outer region, which later becomes clearly separated as the cortex, the radial arrangement of cells is particularly prominent. Directly beneath the stem tip, cell division is less evident than in the lateral surface regions, and parenchyma and procambium mature here with limited meristematic activity.

The leaf traces which cross this outer meristematic portion of the stem, almost at right angles, are stretched and show destroyed protoxylem; most of the bundles forming the irregularly branched part of the stem network mature well below the stem surface and form scalariform xylem elements only.

The evidence of active radial growth in the surface layers of the stem usually disappears beyond the base of about the sixth or seventh leaf. The outer stem region in which storied cells are most conspicuous becomes limited on its inner surface by a layer of cells in which periclinal divisions continue to take place. Where this layer is first conspicuous—beneath the fifth to eighth oldest leaf, varying with the age of the plant—the cortex becomes sharply delimited from the central cylinder. Nearer the stem apex, where no well-defined layer of dividing cells is present, the cortical region can be

most readily distinguished from the central cylinder by the presence of more numerous periclinal divisions and the absence of periclinally directed procambial strands.

The layer of meristematic cells which separates the cortex and central cylinder gives rise to a tissue several cells thick. The innermost layers of this tissue form vascular elements which, except for openings through which leaf traces pass, constitute an almost continuous vascular surface at the outer limit of the central cylinder. The root traces connect to the exterior of this surface, and the vascular bundles of the central cylinder to its interior.

Cells on the outer surface of the layer of dividing cells develop into the stem endodermis, which becomes continuous with all the root endodermal layers (plate 8, B). This endodermis and the vascular tissue formed on the inner side of it are separated by 2 to 4 layers of parenchyma.

The layer described above contributes little to total stem growth. The stem grows primarily from the rather uniformly distributed cell divisions in the young cortex and central cylinder.

The photographs in plate 7 show the layer of dividing cells near the garlic stem tip at A, and two stages in the development of the endodermis at B and C. As the rather poorly defined layer at A becomes older, cells on its outer surface, for the most part in a uniseriate layer, may be distinguished from the surrounding cells by denser protoplasts (B). Finally the walls of these cells lignify, either wholly or in part (C). Where the cells of the endodermis are sufficiently mature to show a lignin reaction (phloroglucinol and HCl), they also absorb fat stains, so that the general pattern for the two stains is the same. With neither of these stains is there any evidence of Casparian strips in early stages of development. Because these are absent, the term endodermis is used in a broad sense. Guttenberg (1943) describes similar layers found in some of the grasses as "endodermoid" and Krauss (1948), in describing the pineapple, uses the terms "peripheral sclerenchyma" or "endodermis-like cells." Because these terms are noncommittal, and because this layer in garlic corresponds in position to typical endodermal layers in other monocotyledonous stems, the author prefers the term endodermis.

Mangin (1882) studied the development of stems and adventitious roots in a great number of monocotyledons, and concluded that the meristematic layer between the cortex and central cylinder was present in essentially all of them, at least in a modified form. He termed this the net-forming layer (*couche dictyogène*) since it forms the vascular network limiting the central cylinder. He stated further that the adventitious roots arise from the net-forming layer, except for the root cap which develops from the stem cortex. The endodermal layer, at least in most species, was considered a derivative of the innermost cells of the cortex. Mangin spoke of the network of vascular tissue limiting the central cylinder as an entity in itself, uniting, on the one hand, with the traces of the adventitious roots, and, on the other, with the lower ends of the leaf traces. Because the root traces are joined to this layer, rather than directly to the leaf traces, Mangin termed it the root-bearing network (*réseau radicifère*). Whether the endodermis in garlic is a derivative of the net-forming layer or the cortex is not clear. It develops in the region where these two meet, and, as indicated in plate 7, A and B, the line of de-

marcation is indistinct. As noted above, Mangin considered the endodermis as the inner layer of the cortex, and stated that in some plants it develops where the net-forming layer is absent. Krauss (1948) stated that in the pineapple, the corresponding layer (which she preferred to call peripheral sclerenchyma, rather than endodermis), is derived from the net-forming (dictyogenous) zone. She considered it the outermost layer of the stele.

Hoffman (1933) did not mention the presence of an endodermis or an endodermis-like layer in the onion bulb. We have made fresh sections of the stems of mature dormant bulbs of two varieties and in both there was a uniseriate lignified (phloroglucinol and HCl) layer around the older part of the vascular cylinder. This layer was continuous with the root endodermis and clearly corresponds to the layer which we have termed the endodermis in garlic, though it appears to lignify much less.

The young adventitious roots of garlic appear on the upper surface of the stem. The root shown in plate 6, A, for example, is about 3 to 4 nodes farther removed from the stem tip than are root primordia when first visible. Root primordia appear to have no particular positional relation with adjacent leaves, except that, in the cortex, and in their outward path through the leaf bases, they alternate with the leaf traces. The irregularity with which roots are sometimes produced is evident in the mature clove (plate 5, B).

The youngest roots we have observed appear to arise from a group of dividing cells which are near, or perhaps a part of, the net-forming layer (plate 8, C). In primordia with clearly organized tips, the net-forming layer connects with the central cylinder of the root (plate 8, A), and from observations on older roots it is evident that this connection is associated with the union of the stem and root endodermal layers. As previously mentioned, the vascular tissue of the root connects with the root-bearing network (plates 8, B and 5, A). In the region of the root base, the root-bearing network and the stem endodermis differentiate only after the root is fairly well formed. The cortex of the adventitious root ends rather abruptly in the stem cortex. This is shown well in cleared slices (plate 3, A and B).

The initiation of adventitious roots in garlic has not been determined in more detail than outlined above. As Krauss pointed out (1949), our knowledge of the origin of roots in the monocotyledons in general is meager, and among the alliums this is also true. Falkenberg (1876) stated that the roots of the onion arise from the active layer (net-forming layer of Mangin) but gave little supporting evidence. Hoffman (1933), in describing the origin of roots in the onion, stated, "Although the pericycle is not distinguishable as a single layer, it is in this region of the stem that the stele of the adventitious root originates." A pericycle is not indicated in any of Hoffman's figures, nor does he give any further description of it. Apparently he inferred the presence of a pericycle because of root initiation, even though, as he indicated, it could not be distinguished. Both Falkenberg (1876) and Mangin (1882) noted the functional similarity of the layer beneath the stem endodermis to the root pericycle, but neither applied this term to it. Krauss (1948, 1949) concluded that there is no pericycle in the pineapple stem. Her concept of this tissue appears to be based almost completely on its functional nature, which is quite contrary to Esau's (1943) ontogenetic concept.

V. STRUCTURE OF THE FOLIAGE LEAF

Epidermis

Details of the uniseriate epidermis of the leaf blade may be seen in figure 8. Cell shape, and disposition and relative frequency of stomata, are shown at A, and details of the guard cells and orifice at B and C. The cuticle, as shown in C, extends through the orifice and around the under side of the guard cells.

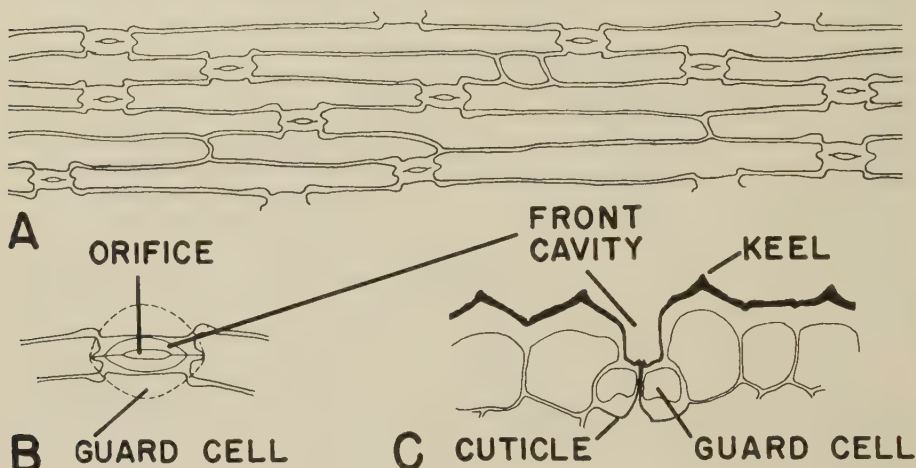


Fig. 8. Epidermis of the foliage leaf blade. A, surface view, showing cell shapes and disposition of stomata. B, surface view of a stoma. C, section through a stoma. A, $\times 170$; B and C, $\times 370$.

A sharp cuticular keel runs lengthwise on the surface of each cell, and, though not indicated in A, may be conspicuous in surface as well as in cross-sectional views. There are no trichomes, except along the leaf edge where single cells form rather blunt serrations. The upper and lower epidermal layers of the leaf blade are essentially alike.

Stomata are lacking, or nearly so, on the inner and outer surfaces of the leaf sheath, but the epidermal cells proper on these surfaces are shaped like those of the leaf blade. Their inner tangential walls may be thickened more than those of the cells of the leaf blade, and in some areas on the outer surface of the sheath, certain cells may thicken and lignify on all sides, contrasting markedly with the intermixed thin-walled cells. This epidermal sclerification in the foliage leaf sheath is similar to that described below for the protective leaf of the clove, but usually involves only scattered cells, or may be absent.

Mesophyll

The general organization of leaf mesophyll can be seen in plate 9, which shows a cross section of a foliage leaf blade (A), and a leaf sheath (B). The chlorenchyma of the leaf blade is shown in more detail in plate 10. In this plate, the well-developed palisade tissue, mostly a single cell deep, is shown in tangential section at A, in radial sections, lengthwise of the leaf at B, and

across the leaf at C. The palisade layer abuts onto elongate, undulate chlorenchyma cells (plate 10, B and C) which have only a moderate amount of intercellular space, and farther inward become less irregular in shape, longer, and devoid of chloroplasts. In the leaf center, large irregularly distributed intercellular spaces may occur. The mesophyll of both surfaces of the leaf blade is arranged in essentially the same manner (plate 9, A).

The mesophyll of the leaf sheath (plate 9, B) consists of elongate parenchyma cells of uniform shape. The presence of chloroplasts in the leaf sheaths is variable, but no palisade tissue is found.

Laticifers⁵

The mesophyll of the garlic foliage leaf contains a large number of laticifers, each consisting of several much-elongated cells set end to end. These long rows of cells run parallel to one another and lengthwise of the leaf blade and sheath. Their position and frequency in the foliage leaf are indicated in plate 9, A and B, plate 10, C and D, and plate 11, A. The laticifers are difficult to identify in cross sections of the sheath (plate 9, B), but their conspicuous protoplasts and the relatively small size of the intercellular spaces contacting the laticifer wall help to distinguish them. In the leaf blade, the side of the laticifer directed toward the leaf epidermis is connected, quite frequently, to the inner ends of the palisade cells. Longitudinally, they extend to the leaf tip where they end blindly. While they are present near both surfaces of the leaf blade, those near the adaxial surface end in the ligule region; in the sheath, they are found only near the outer surface. In cross section they appear to be separated from the epidermis by one or two parenchyma cells (plate 9, B). The laticifers end in the leaf base and are absent from the stem.

While the spacing of the laticifers with respect to the epidermis is similar in both garlic and onion, Menz (1922) pointed out that they have a strictly subepidermal position in the *Molium* section of the genus.

The tangential section of the leaf blade (plate 10, D) shows the cross walls where laticifer elements meet. In the mature leaf blade, the elements are about 2 mm long, which would make the elements of plate 10, D, at the magnification used, about 6 inches long. The cross walls are commonly set at a slight angle, as shown, and the joined ends usually bulge laterally. Haberlandt (1914, p. 305) considered this bulging a development associated with translocation. In surface view, the end walls commonly have 5 to 7 large, well-defined pits. In contrast to the observations of Rendle (1889) on onion laticifers, the laticifers of garlic are conspicuously pitted wherever they contact parenchyma cells. No callose was observed on the cross walls (aqueous resorcin blue on fresh sections) (cf. Rendle, 1889).

Leaf Blade Lacunae and Collapse of Leaf Sheath Tissue

Numerous longitudinal cavities large enough to be easily visible to the naked eye are present in the mesophyll of the mature leaf blade. In young leaves, there are intercellular air spaces of moderate size (plates 9, A and

⁵ Dr. Katherine Esau suggested the term *laticifer*, which is used here in place of *laticiferous ducts*, *latex vessels*, etc.

11, B). However, lacunae are formed, in the main, by the dissolution of longitudinal rows of cells. Frequently the breakdown occurs along only one side of a row of cells, so that the walls of the lacunae consist of portions of longitudinal walls of the cells from which they are formed (plate 11, C). This breakdown is orderly to the extent that definite tubes are formed running lengthwise of the leaves. Strongly chromatic material is evident in the intercellular spaces of leaves in which cell wall dissolution is starting (plate 9, A, at *chr mat*, and also at extreme right in this same picture).

Cell destruction in leaf sheaths consists of collapse of the parenchyma beneath the adaxial epidermis, as indicated in plate 9, B and C. This collapse begins early and continues until, in a mature dry sheath, only the mechanically resistant outer epidermis, the vascular tissue, and a few parenchyma cells adjacent to these structures remain.

It appears that this cellular collapse in the sheaths contributes to the weakness of the false stem, and ultimately leads to its breaking or bending over at maturity. This mechanism is quite different from the one proposed by Heath (1945) for the bending of the tops in mature onions. The process of maturing and breaking of tops needs to be carefully checked in the two species.

Vascular Structure

The vascular traces of the leaves enter the leaf bases, as described under stem anatomy, and follow an essentially parallel course for the length of the sheath and the blade. Cross sections of the sheath usually show small bundles alternating with larger bundles, though this is by no means constant. Frequently small bundles run transversely between adjacent parallel veins, usually at an angle. A few of the smaller bundles running lengthwise of the sheath branch from the larger bundles. The bundles appearing in plate 9, B and C, are typical of the leaf sheath.

In a transverse section of the leaf blade the vascular bundles are seen to be arranged in two rows, one near each leaf surface, rather than in a single row as in the sheath. This arrangement may be seen in plate 9, A, which shows three small bundles near the adaxial leaf surface (lower side in photograph) and two bundles, one small and one large, near the abaxial surface. The pattern indicated here is more or less continuous across the leaf blade; small and large bundles alternate near the lower surface, and all bundles are small near the upper surface. The xylem and phloem of the lower-surface bundles are oriented in the usual way, but the bundles near the upper surface are inverted, i.e., have abaxial xylem.

The transition from the single row of bundles in the sheath to the double row in the blade occurs in the blade-sheath junction, usually at or slightly below the ligule region. Here the large and small bundles near the lower leaf surface appear to be directly continuous with the large and small bundles of the sheath, while the small inverted bundles branch from these toward the upper leaf surface. Almost all sheath bundles branch at least once, and, with few exceptions, the two branches come to lie opposite each other in the leaf blade, frequently surrounded by a common parenchymatous bundle sheath.

It is interesting to note that the arrangement of the vascular bundles of the leaf blade in two rows, as illustrated by garlic, and apparently also by

onion (Hayward, 1938), is by no means common to all Alliums. In several species the bundles of the blade occur only in a single row, as in the sheath, and all have adaxial xylem. Menz (1910) discussed this variation from a taxonomic standpoint, and Arber (1920) and Menz (1922) surveyed many alliums for bundle orientation, particularly with reference to Arber's phyllode theory of monocotyledonous leaves.

Plate 11, A, shows, at a greater magnification, a bundle from the leaf section in plate 9, A. Fibers are present near both the xylem and the phloem. These fibers are frequently continuous across the center of the leaf between paired bundles. Bundle fibers may be present in the upper leaf sheath, but have not been observed in the part of the sheath surrounding the bulb. As in the corn leaf (Esau, 1943), many of the small bundles are formed late and show no protoxylem lacunae, which are present in the large bundles.

The bundles of the foliage leaf are surrounded by a sheath of large parenchyma cells, mostly a single layer thick. This layer is especially conspicuous in the drying leaf sheath where, at least from the appearance of fixed material (plate 9, C), its cells maintain their protoplasts after those of the surrounding parenchyma are dead. It is less conspicuous in the mature leaf sheath (plate 9, B) and still less so in the leaf blade (plate 9, A). Generally this layer can be distinguished from adjacent parenchyma by the heavy-staining, frequently granular cytoplasm, especially on the phloem side of the bundle. As noted for corn by Esau (1943), intercellular spaces are small or lacking among sheath cells or between them and the vascular cells.

VI. STRUCTURE OF THE PROTECTIVE LEAF

Surrounding each clove is a leaf which, because of its tough, hard surface, is called the protective leaf (plate 2, E, 1). Though the protective leaf has no connection with any part of an abscised clove (fig. 7, B and C), it is difficult to remove because it is tough and usually closely appressed to the clove surface. It ordinarily remains around the clove when the bulb is broken apart.

The portion of the protective leaf which surrounds the clove is almost entirely sheath; the much-reduced blade is usually only a few mm long (plate 2, E, 1). The protective leaf contains no chlorophyll and does not store food. Except for the outer epidermis, which lignifies to form a continuous sclerotic layer, its anatomy is much like that of the sheath portion of a foliage leaf. All cells of the sheath, except for the outer epidermis and the lignified xylem elements, collapse at maturity. This collapse progresses from the inner to the outer surface (fig. 9, A) as does the collapse of the foliage leaf sheath (plate 9, B and C). Vascular bundles run lengthwise of the sheath, and in the apical half or third numerous cross-veins may be present. The laticifer system is present and resembles that of the foliage leaf sheath.

The shape of the epidermal cells from a mature, dry protective leaf is shown in surface view in figure 9, B. In these mature cells the lumina are quite small. Figure 9, A, is drawn from a cross section of a nearly mature leaf which has not yet dried. The epidermal sclereids are about 0.5 mm long by 0.03 mm wide (tangentially). Near the clove base they may be twice this

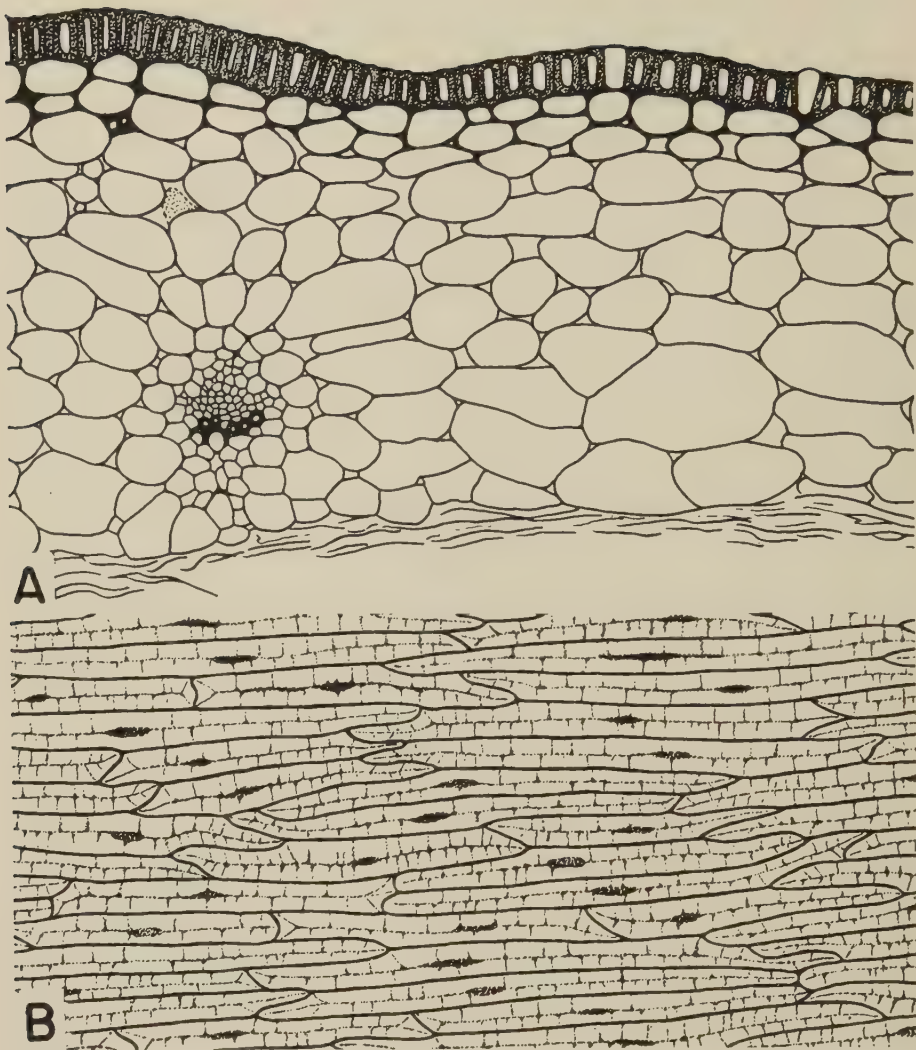


Fig. 9. A, a cross section of a nearly mature protective leaf, showing the sclerified abaxial epidermis. As this leaf dries, the parenchyma continues to collapse toward the abaxial surface. B, a surface view of a mature epidermal layer. These sclereids are more mature than those shown in A, and the lumina have nearly disappeared. $\times 90$. (Drawings by Dr. Katherine Esau.)

length and at the apex several times shorter. Occasional cells are much wider. The epidermis is covered by a relatively thin, smooth cuticle. Stomata are practically lacking except on the much-reduced blade, where they may be surrounded on all sides by lignified cells.

Immediately beneath the lignified epidermis is a layer of thick-walled, nonlignified, isodiametric cells which contain much of the pigment giving the pink color to the cloves of Late garlic. The protective leaves of the small

cloves near the center of the bulb may have a lignified epidermis near the base only, or lignification may be almost entirely absent. Where lignification is not complete, the epidermis usually consists of a mixture of heavily lignified and nonlignified cells. This is the type of outer epidermis found occasionally on the foliage leaf sheaths, and, on plants grown in the field during the winter, it has been observed particularly on the sprout leaf.

Protective leaves, i.e., thin sheaths surrounding storage leaves and usually possessing well-developed mechanical tissue, are quite common among the alliums, and have been described for many species (Tavel, 1887; Baldrati, 1897; Menz, 1910, 1922). These studies, undertaken primarily for taxonomic purposes, are anatomically somewhat superficial. Perhaps the most thoroughly studied species are members of the section *Molium*. Here the sclerotic layer of the protective leaf is reported to be the inner epidermis (*Allium chamaemoly* L. and others), a layer beneath the inner epidermis (*A. moly* L.), or beneath the outer epidermis (*A. pendulinum* L.), or a combination of these, or none (*A. multibulbosum* Jacq.). In other sections, the fibrous tissue remaining after natural retting of outer leaf bases may serve as protective layers (*A. victorialis* L.). In the sections *Macrospatha*, *Rhiziridium*, and *Schoenoprasum*, the outer epidermis is usually sclerified (Menz, 1910). There is little information, however, about the *Porrum* section to which garlic belongs. Tavel (1887) stated that the protective leaf of *A. scorodoprasum* L. has a lignified epidermis, and his figures suggest that it is similar to garlic.

Menz (1910) stated that in both *A. ampeloprasum* L. and *A. porrum* L. the epidermis is thin-walled. This seems hardly possible for *A. ampeloprasum* L., since the material we have grown has tough, sclerified protective leaves.

VII. STRUCTURE OF THE STORAGE LEAF

In the garlic clove, almost all the reserve food is stored in a single leaf, the storage leaf. As indicated in table 1, this leaf makes up, by weight, approximately 80 per cent of the clove and 75 per cent of the mature, trimmed bulb. However, its functional life is short after the cloves are planted. It is depleted of food and dries or rots away by the time the young plant is several inches high (fig. 3, A and B).

This storage leaf is strikingly modified in form as well as in function. It consists almost entirely of sheath, is tubular in shape, and surrounds the developing foliage leaves (plate 2, E. 2). The opening at the tip through which the enclosed leaves emerge is asymmetrical, with a slit sometimes extending several mm down one side. The tip portion represents a much-reduced leaf blade, as suggested by its asymmetry and by the presence of scattered stomata on its surface. However, neither a change in texture nor the presence of a ligule gives any evidence of a sheath-blade junction.

Epidermis

The outer epidermis of the storage leaf (plate 12, B) is thin and delicate—much more so than the epidermis of the foliage leaf. It has little tensile strength and cannot be stripped from the leaf except in very small pieces.

This weakness is not surprising since the storage leaf is closely invested by the protective leaf. The inner epidermis is equally delicate, but can be easily stripped in the mature clove because it has underneath it several layers of collapsed parenchyma.

The cells of the outer epidermis are variable in shape and are arranged in somewhat irregular rows. These cells average some 0.06 mm long by 0.03 or 0.04 mm wide. Cells of the inner epidermis are the same width but roughly twice as long.

Stomata are absent from the inner epidermis of the storage leaf. On the outer epidermis, isolated stomata can be found and, at the extreme apex and base of the leaf, they may be moderately abundant. Here they are irregularly scattered among the epidermal cells, most of which are isodiametric and show no evident arrangement in rows.

Mesophyll

The general appearance of the storage parenchyma can be seen in plate 12, A and B. The parenchyma throughout the leaf is quite uniform. The heaviest food concentration appears, on the basis of staining, to be near the outer surface. Most storage cells are quite uniformly filled with finely granular material. Isolated starch grains can be found, but they are very infrequent. The collapse of cells under the inner epidermis resembles that in the sheaths of the protective and foliage leaves.

Laticifers

The laticifers of the storage leaf run longitudinally near the outer epidermis (plate 12, A and B). Measurements of some 20 laticifer elements from mature storage leaves gave an average length of about 0.5 mm (range 0.28 to 1.0 mm), with about 0.25 mm between adjacent parallel laticifers.

Vascular Structure

It can be seen from plate 12, A, that the vascular bundles of the storage leaf are most numerous in two regions: near the outer surface of the leaf, and around the central opening. From longitudinal sections of the storage leaf, it is evident that bundles of these two series are connected separately to the stem network of the clove (fig. 7, A; plate 5, A; plate 4). In plate 5, A, these two series of bundles entering the storage leaf can be compared with the single series entering the base of the foliage leaf. Once within the storage parenchyma, both series branch freely and bundles may be found running in many directions through the storage tissue.

The two series of vascular bundles in the storage leaf recall the similar situation in the foliage leaf blade. The resemblance, however, is apparently superficial, since those in the storage leaf differ from those of the foliage leaf in that they enter the stem as independent bundles, and in that their xylem and phloem are oriented in the usual way. While the vascular structure of the storage leaf deviates from that of the foliage leaf sheath, it seems simplest, for the present, to interpret the storage leaf as a modified sheath.

The vascular bundles of the storage leaf have relatively much less xylem than do those of the foliage leaf. This is shown in plate 12, A, where, in the marked-off area of the storage leaf, those bundles indicated by small circles lack xylem elements. Of the 55 bundles in this delimited area, 22 had phloem only. In these 22 are included most of the bundles occupying the area between the two bundle series. The remaining bundles averaged, in cross section, 3.26 xylem elements per bundle.

Of the bundles with xylem, only the largest, such as the one shown in plates 12, B and 13, A, have areas of collapsed protoxylem and protophloem. In most of the bundles (plate 13, B) there is no collapsed xylem, and the intact elements show little evidence of having elongated after reaching maturity.

The parenchymatous bundle sheaths in the storage leaves are more conspicuous than those in other leaves. They are most readily distinguished from the surrounding parenchyma by their granular fixation image. In contrast to those of the foliage leaf, these sheaths are quite irregular in thickness, being absent in some spots and several cells thick in others. In fresh sections the sheath cells give strong protein reactions with biuret, Millon's, and other reagents. Braecke (1921) studied the microchemical reactions of the storage leaf, and her paper should be consulted for details.

No lignified cells, or cells with thickened walls, other than the conducting elements of the xylem, are present in the storage leaf.

VIII. STRUCTURE OF THE ROOT

Apical Meristem

The region of initiation of the tissues of the garlic root is shown in longitudinal section in plate 14. The organization of the root meristem, as it appears in *median longitudinal sections*, is briefly as follows. The vascular cylinder (including the pericycle) may be traced toward the apex, where it appears to arise from three or four initial cells. Lateral to the initials of the vascular cylinder are some 4 to 5 initials which give rise to the cortex and epidermis. The root cap has a column of 8 to 10 longitudinal rows of cells. At the edges these divide periclinally, extending the cap laterally. The shape and position of the initial cells seem to provide no evidence that these groups of initials are distinct from one another.

Hoffman (1933) described the histogens of the root tip of onion as fitting Treub's modification of Janczewski's type 2 (Hayward, 1938). This implies two distinct groups of initials, one giving rise to the vascular cylinder, and the other to the cortex, endodermis, and root cap. A comparison of onion and garlic root tips shows little difference in organization. Roots of the two are shown together in plate 15, with the limits of the vascular cylinder indicated. The onion tip shown here agrees quite well with those drawn by Hoffman (1933). In neither plate 14 nor 15 do there appear to be two distinct groups of initials. Foster (1949) has discussed the difficulties of fitting root meristems into Janczewski's morphological types. Further studies on the garlic and onion root tip are needed, especially using criteria in addition to cell shape and position to determine cell-lineage.

Maturation of Root Tissues

In longitudinal sections of roots, the phloem is recognizable quite early through disappearance of the sieve tube nuclei. Measurements made on 6 root tips showed these nuclei disintegrating at an average of 1.3 mm from the root apex (range 1.1 to 1.5 mm). The first easily recognizable stage of vessel formation, the differential staining or accumulation of cytoplasm in specific areas on the cell walls prior to secondary thickening, was observed in 4 roots at an average of 10.1 mm from the tip (range 7.3 to 12.3 mm). At about this level, or slightly farther from the apex, the Casparian dots or strips in the endodermal cells are first evident. Most of these data were obtained from roots grown in water.

The appearance of roots in cross section at two stages of development is shown in plate 16, A and B. As is evident from the picture at B, the inner tangential and radial walls of the endodermal cells become very conspicuously thickened at maturity. The Casparian strips and dots which are evident in younger cells can no longer be seen. The garlic root has no passage cells such as Haberlandt (1914, p. 352) shows for *Allium ascalonicum* L. The effect of environment on the development of the root endodermis in garlic has been reported by Van Fleet (1942).

Old roots, especially near their bases, may show considerable sclerification of the outer cortical cells. In younger roots, the outer layers absorb fat stains readily, but they stain only weakly for lignin.

SUMMARY

The gross structure of the garlic plant is described, with anatomical details of the vegetative stem, the leaves, and the adventitious roots. Several experiments on the growth responses of garlic under controlled photoperiod and temperature are reported. The literature is reviewed, with special attention to the anatomy of other allium species.

The young garlic plant, prior to bulbing, is similar in structure to the common onion. At its base is a small, flat stem which bears numerous adventitious roots and the foliage leaves. The long, sheathing bases of the latter form a conspicuous false stem, from which diverge the two ranks of flat, keeled leaf blades.

The mature, dry garlic bulb is a storage structure particularly well adapted to vegetative reproduction. Each bulb can be separated into many small parts called cloves. These are actually small bulbs, which abscise readily from the main stem. Along with top-sets, which are occasionally produced, they are the sole means of propagation. There are some 10 to 20 cloves in an average bulb; these are produced in groups of 1 to 5 in the axils of the foliage leaves. An average bulb has 6 to 8 foliage leaves bearing axillary cloves, and these leaves are always surrounded by several foliage leaves which bear no cloves.

In a mature bulb, all the foliage leaves of the current season's growth, and the stem and roots as well, die, leaving only the cloves to continue the plant for the next season.

Each of the cloves in a mature bulb consists of a short stem bearing 8 to

10 leaves. The three outermost are strikingly modified in form and function. The outermost leaf, termed the protective leaf of the clove, is a dead, dry, bladeless sheath with a heavily lignified epidermis. This closely invests the rest of the clove and is difficult to remove because of its tough epidermis. Within the protective leaf is a leaf made up of a greatly thickened sheath. This is the main storage structure of the clove and accounts for about 80 per cent of its fresh weight. Next comes a leaf which surrounds and elongates with the foliage leaves, protecting them as they push through the soil when the clove sprouts. This leaf resembles the foliage leaf except that it is bladeless, or nearly so. Its outer epidermis may show considerable lignification, but only after the young plant is well sprouted. Within this leaf are several foliage leaves, decreasing in size to small primordia at the stem apex.

Seedstalks may develop in garlic, though they are uncommon in commercial garlic fields in California. They are borne terminally on the main stem of the plant. Seedstalks always bear small top-sets and usually flowers, though the latter appear to be sterile, and true seeds are unknown. Several attempts to induce seedstalk formation in garlic by low-temperature treatments of bulbs and of plants were unsuccessful.

The structure of garlic is discussed in relation to that of other *Allium* species which have been described in the literature.

Considering the anatomy of the garlic plant in more detail, it is observed that the garlic stem has a well-defined cortex and vascular cylinder, but that the vascular bundles in the stem center do not delimit a pith region. The leaf traces in the stem follow the palm type of arrangement, though abundant anastomoses make it impossible to map completely individual traces in the mature state. Root traces connect only to the well-defined surface of the vascular cylinder, while lateral bud (clove) traces, as well as leaf traces, penetrate into the central cylinder. Except for the root and leaf traces which cross it, the cortex is free from vascular bundles. Older parts of the stem have a lignified, suberized layer, here interpreted as an endodermis, which is continuous with the endodermis of the adventitious roots.

Foliage leaves have a sheathing base, a flat, keeled blade, and a ligule at the blade-sheath junction. Stomata are present on both surfaces of the leaf, and beneath each surface is a well-developed palisade layer. In a transverse section of the blade, there can be seen a row of bundles beneath each surface. The bundles of both of these rows are collateral with the xylem directed toward the leaf center, i.e., away from the nearest epidermis. In the sheath, there is a single row of bundles with the xylem directed toward the stem center, i.e., in the usual way. These bundles connect, in the ligule region, to the two rows of bundles of the leaf blade. Laticifers, consisting of rows of much-elongated cells set end to end, run lengthwise of the leaf a short distance beneath both surfaces of the leaf blade, and beneath the outer surface of the sheath. These laticifers are present in the same relative position in all leaves of the garlic plant, but are absent from the stem and roots. Lacunae develop in the center of the older leaf blades by breakdown of longitudinal rows of cells. In mature sheaths there is a gradual collapse of parenchyma starting beneath the inner epidermis and progressing outward.

The protective leaf of the clove is much like the foliage leaf sheath in structure, except that its outer epidermis consists of thick-walled lignified sclereids.

The storage leaf of the clove has a much-reduced blade and a greatly thickened sheath. The latter differs from the sheath of the foliage leaf in that it possesses two series of vascular bundles (in transverse section, a row near each epidermis) from which other bundles branch in all directions. Many of these are made up of phloem only, and all are normally oriented, as contrasted to those of the foliage leaf blade.

The roots, all of which arise adventitiously from the stem, present no unusual structures. They originate near the stem tip in the boundary region between the cortex and vascular cylinder. The need for further study of the stem tip, especially with reference to root initiation, is pointed out.

The development of plants growing in the field is described. Plants were harvested and dissected periodically during the growing season to determine rate of leaf initiation, time of clove initiation, and the relation of these to bulb formation. For plants grown at Davis, California, cloves began forming in mid- to late April and continued to differentiate throughout May. Bulb enlargement depends on the formation of cloves, and closely parallels their initiation and growth. Observations on plants grown under controlled day length and temperature show that both long days and high temperatures favor bulb formation.

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PLATES

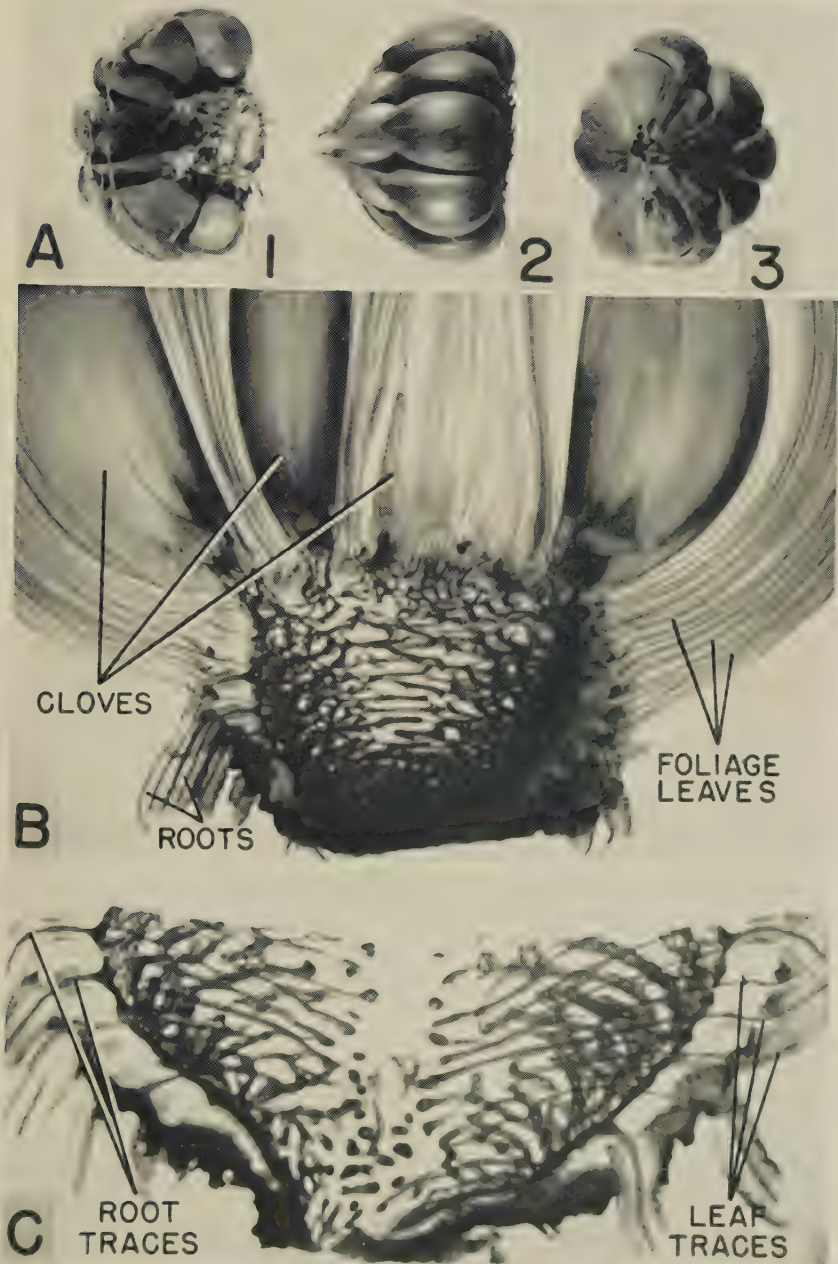
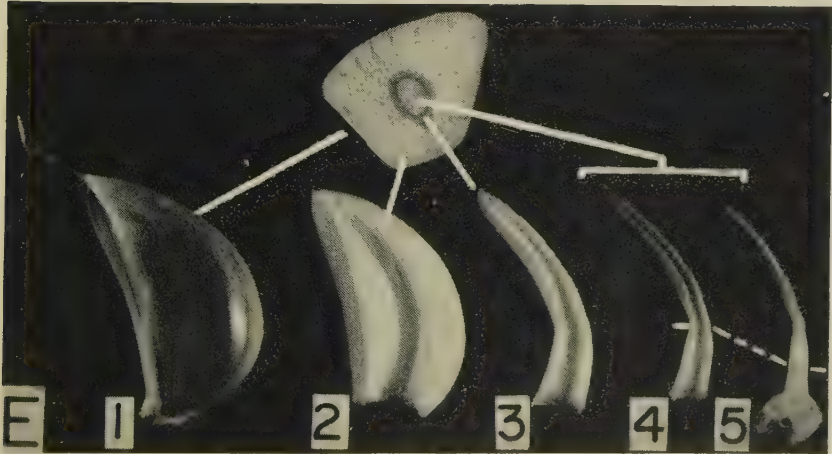
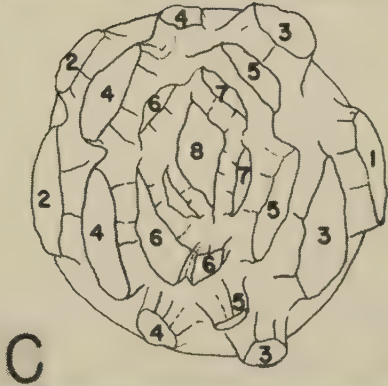
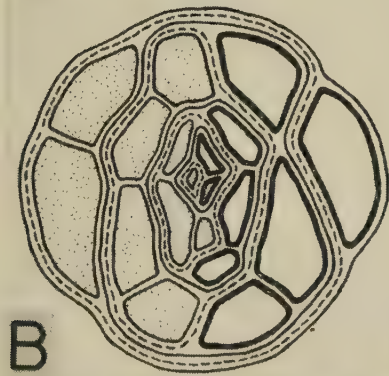
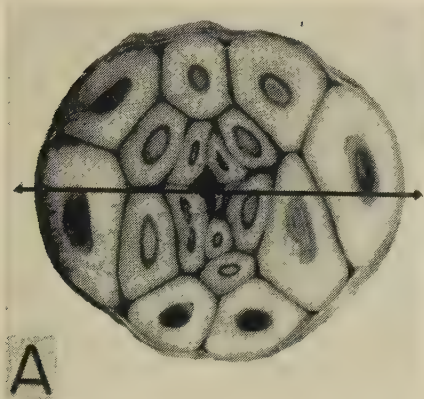


Plate 1. A, partly dismantled mature garlic bulbs showing the arrangement of cloves in the axis of a foliage leaf. B, a cleared longitudinal slice from a garlic bulb. The vascular structure of the foliage leaves, cloves, and adventitious roots can be seen. C, leaf and root traces as they appear in a cleared longitudinal slice of the stem of a young garlic bulb.

Plate 2. The mature garlic bulb and clove. A, transverse surface of a bulb showing the arrangement of cloves. The arrow indicates the direction of the two ranks of leaves above the bulb. B, a drawing from the photograph at A showing the foliage leaf bases surrounding the cloves. C, the stem of the bulb at A after removal of the cloves. The numbered projections are the stem bases from which the cloves abscised. D, a mature bulb cut longitudinally to show the cloves and stem. E, cross section of a single clove with the corresponding parts shown below in longitudinal section as follows: 1, protective leaf; 2, storage leaf; 3, sprout leaf (bladeless); 4, first foliage leaf; 5, second foliage leaf surrounding still smaller foliage leaves, all attached to the stem. The dotted line indicates the lower limit of the leaf blade.



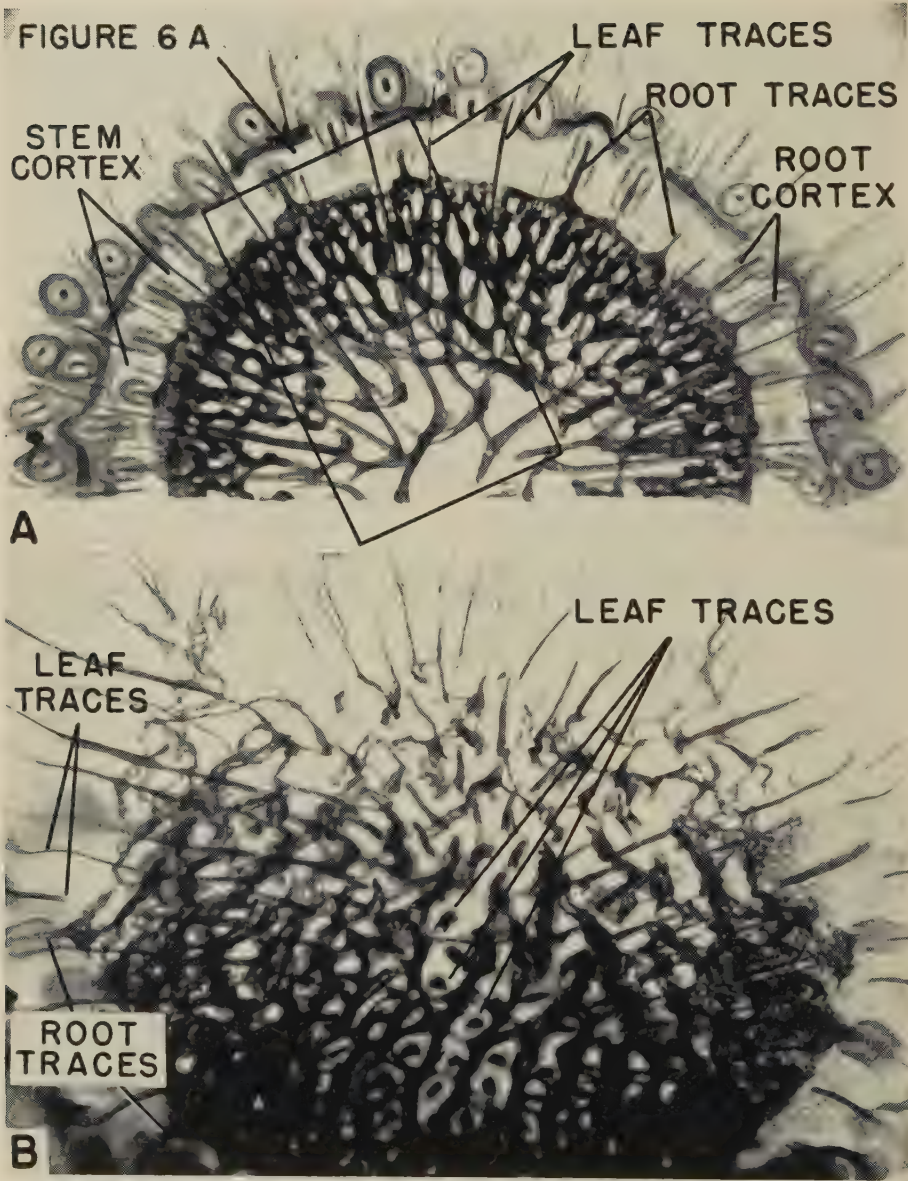


Plate 3. Cleared slices of a nearly mature garlic stem. A, a cross section, not strictly transverse, but slanting downward toward the stem center parallel to the leaf traces (see plate 1, C). A detailed drawing of the portion outlined appears in fig. 6, A. B, a tangential slice near the stem surface.

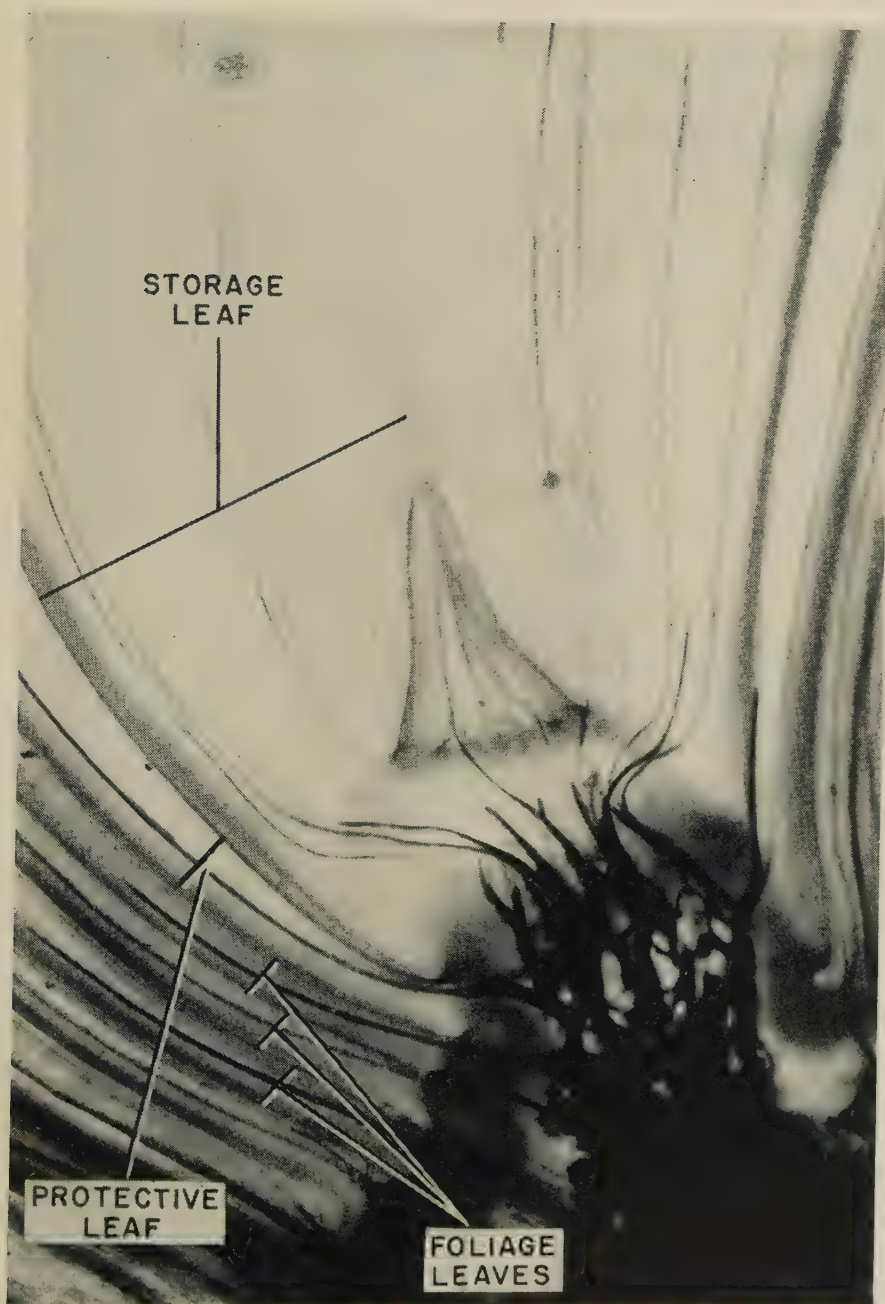


Plate 4. A cleared longitudinal slice through the base of a developing clove attached to the mother bulb. Compare this photograph with the drawing, fig. 7.

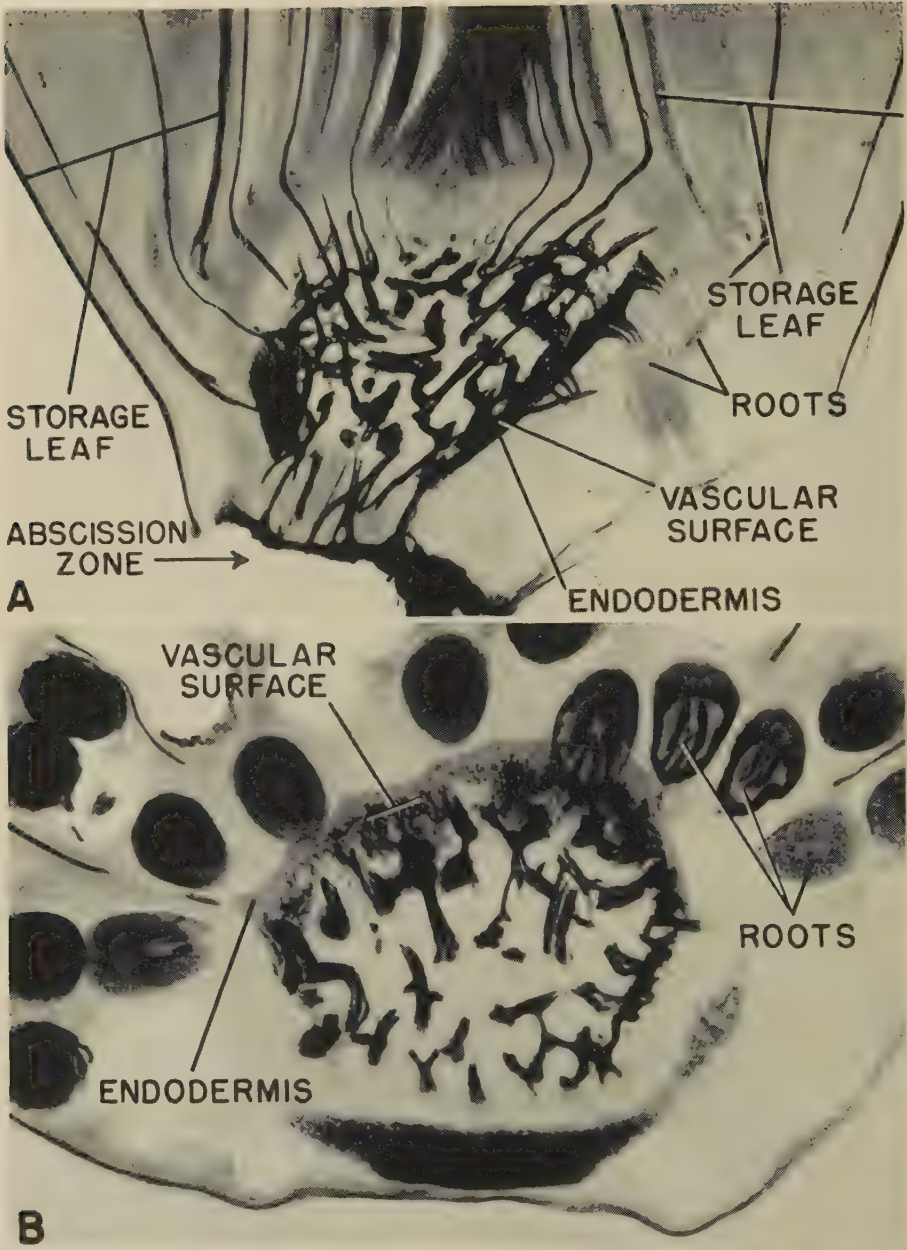


Plate 5. Cleared slices of garlic cloves. The longitudinal section shown at A was cut radially with respect to the mother bulb, and the adaxial side is to the left. In the transverse section, B, the adaxial side is below.

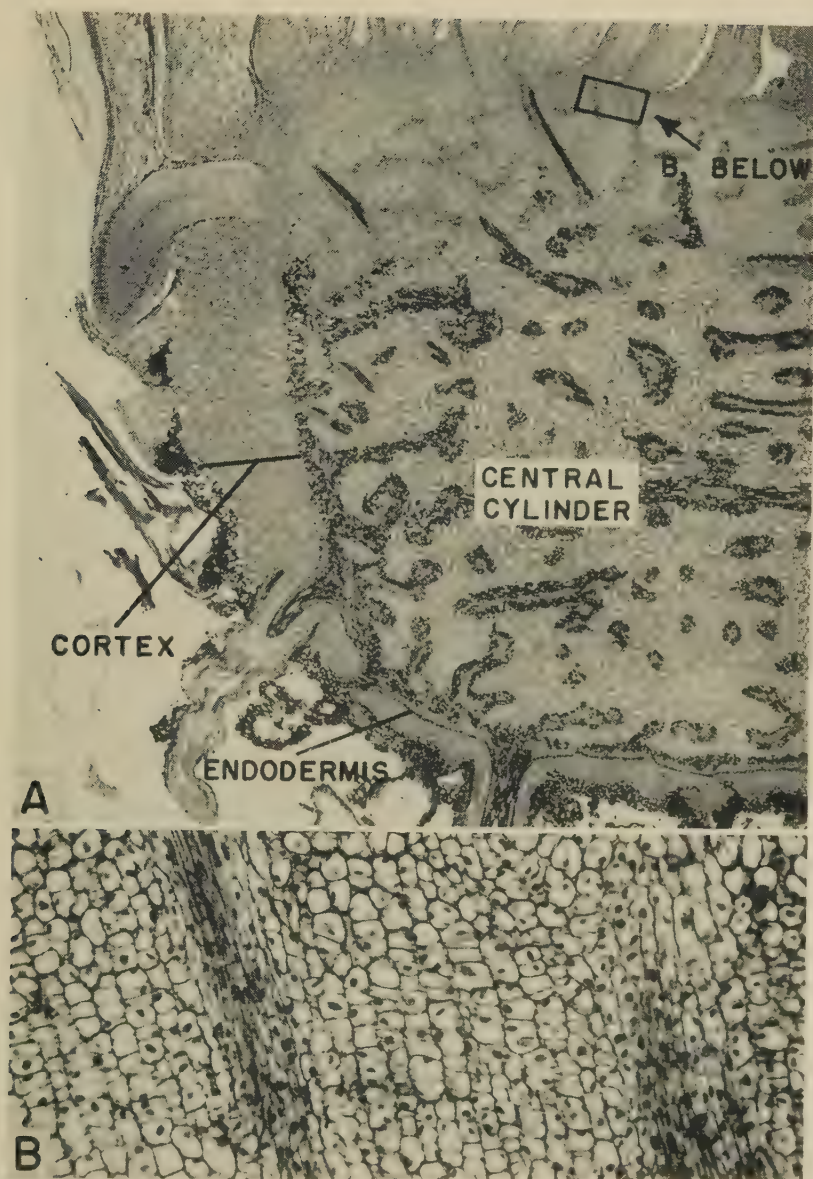


Plate 6. A, a median longitudinal section of the stem of a young plant. The dark regions are mostly lignified tissues. The lignified parts were stained with crystal violet, the unlignified areas with orange G. The meristem region outlined in A is shown in greater detail in B. A, $\times 15$; B, $\times 55$.

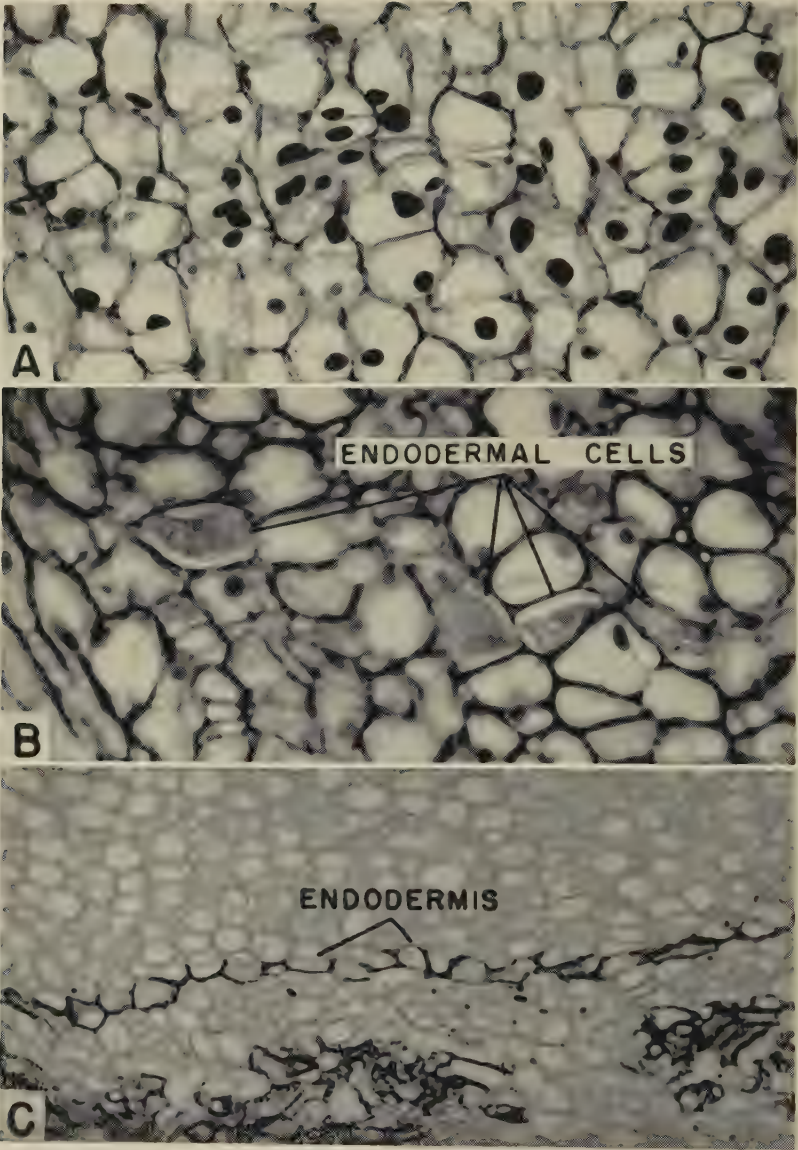


Plate 7. Development of the stem endodermis. A, the layer of dividing cells in the approximate region where the endodermis will appear. B, cells with deep staining protoplasts (orange G) by which the endodermal layer may first be recognized. C, the mature, lignified and suberized endodermal layer from a section stained with crystal violet and orange G. In all three sections the cortex lies toward the top of the plate. A and B $\times 300$, C $\times 160$.

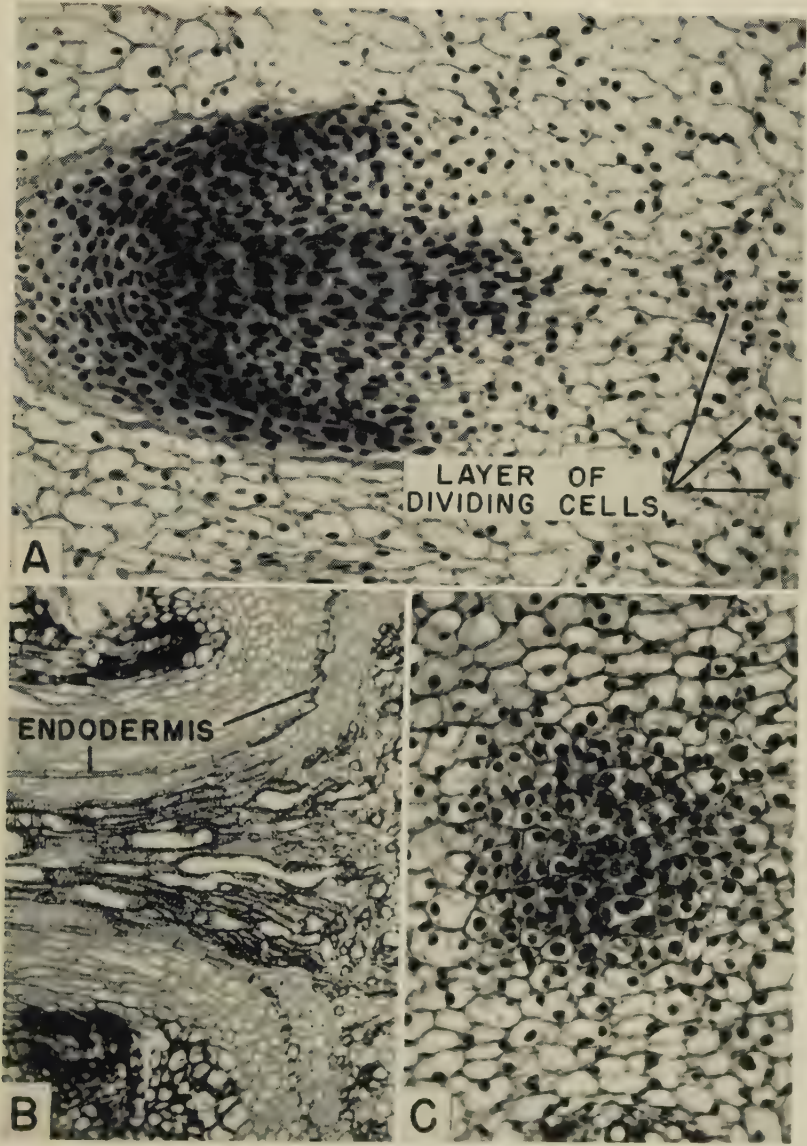


Plate 8. A, a young root, showing its position in relation to the layer of dividing cells. B, the base of a mature root showing continuity of stem and root endodermal layers. This section stained with gentian violet and orange G. C, an early stage in root initiation. The area shown organizes into the root tip. For all three figures, the stem center lies to the right. A and C, $\times 160$; B $\times 80$.

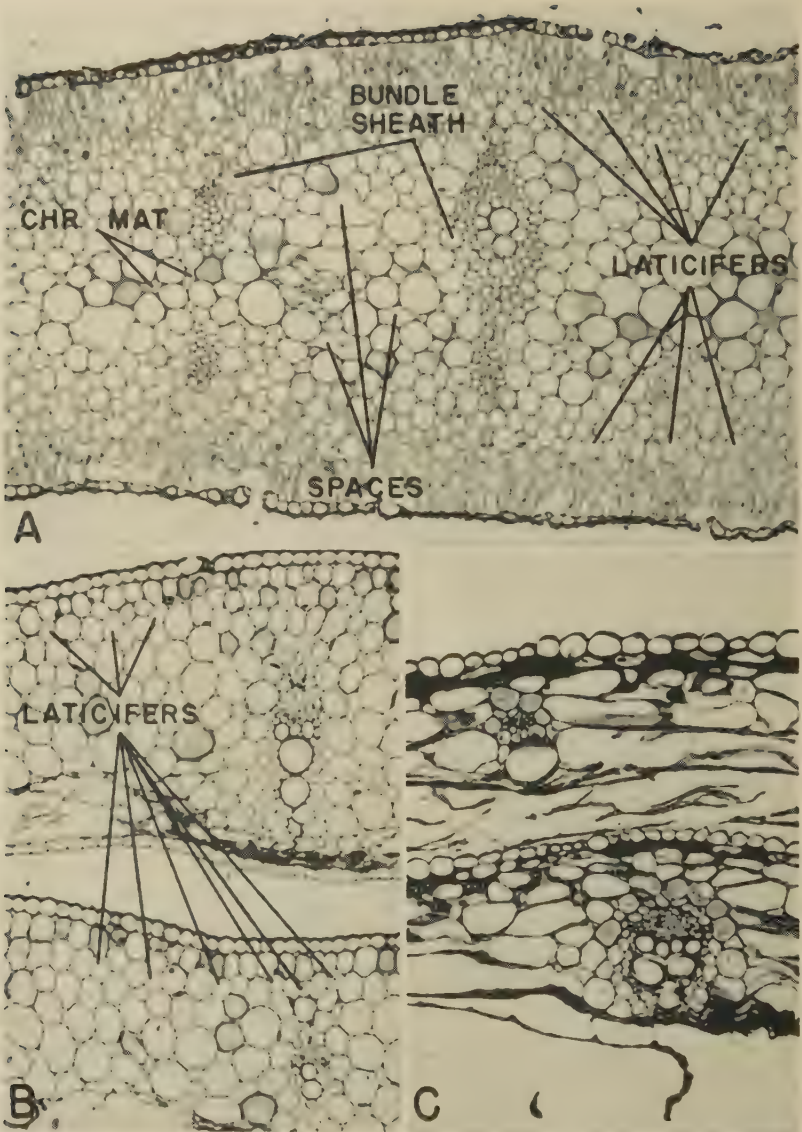


Plate 9. Cross section of foliage leaf blade and sheath. The abaxial surface of the leaf is uppermost in each photograph. A is from the mid-portion of a leaf blade and shows 5 vascular strands. The chromatic material (chr mat) is from cell wall dissolution and marks the beginning of lacunae formation. Note the symmetrical disposition of palisade cells and laticifers with respect to both leaf surfaces. The sections in B are from mature leaf sheaths 19 cm above the bulb base. Palisade cells are absent, laticifers are present only near the outer surface, and cell collapse is evident beneath the inner epidermis. C shows drying sheaths (from around a bulb) in a late stage of collapse. All $\times 78$.

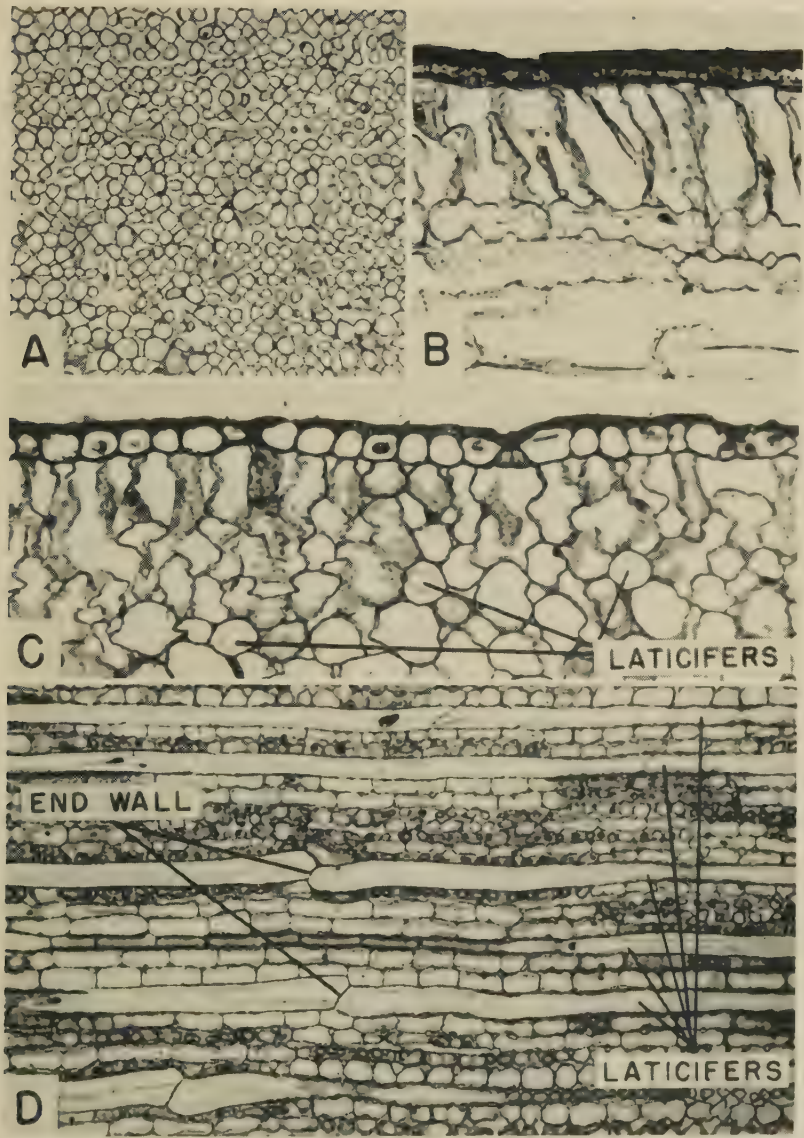


Plate 10. Sections of the foliage leaf blade showing chlorenchyma and laticifers. A, tangential section through the palisade layer. In B, a longitudinal radial section, the undulate chlorenchyma cells can be seen beneath the palisade cells. C is a transverse radial section showing chlorenchyma and laticifers. D is a tangential section a little deeper in the leaf than A, and illustrates the lateral spacing of laticifers. A and D, $\times 78$; B and C, $\times 225$ approx.

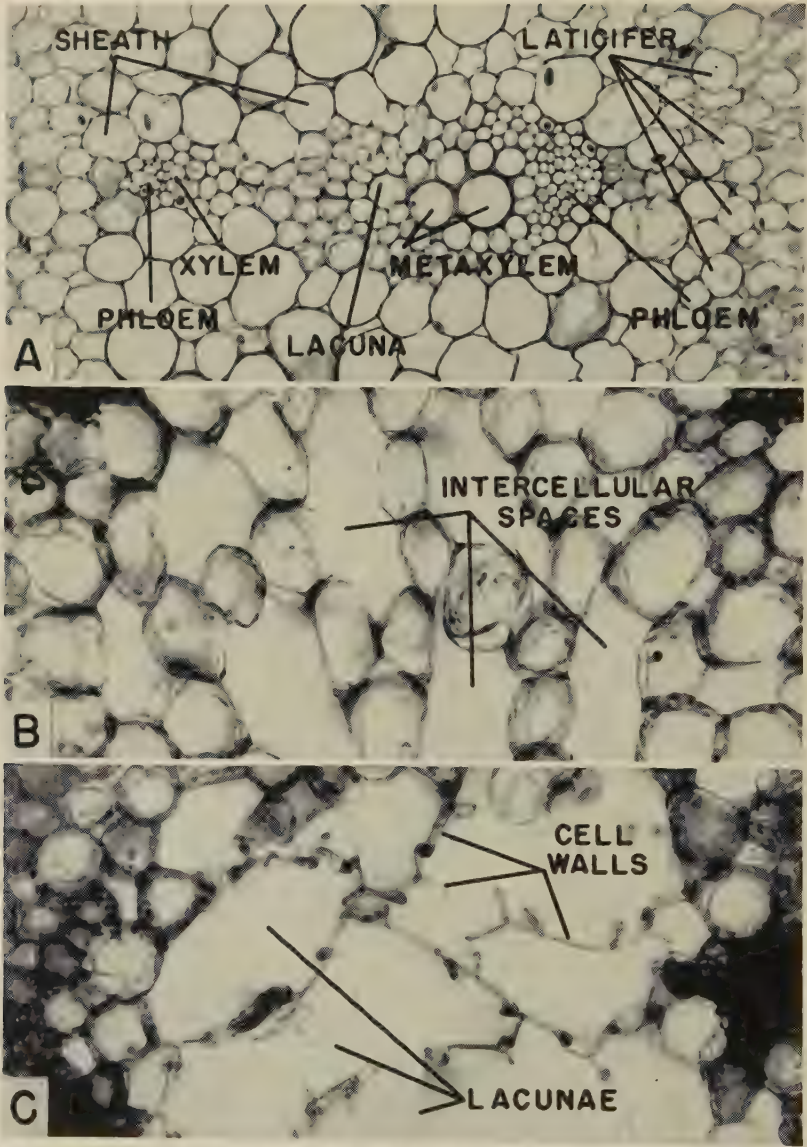


Plate 11. A is an enlargement of the double leaf bundle shown in plate 9. A. The abaxial leaf surface is to the right. B is a fresh section of an area of extensive intercellular spaces in the central mesophyll of a leaf blade prior to lacunae formation. C is a fresh section across well developed lacunae. The septae are made up of walls of cells which have opened and lost their contents. A, $\times 158$; B and C, $\times 175$ approx.

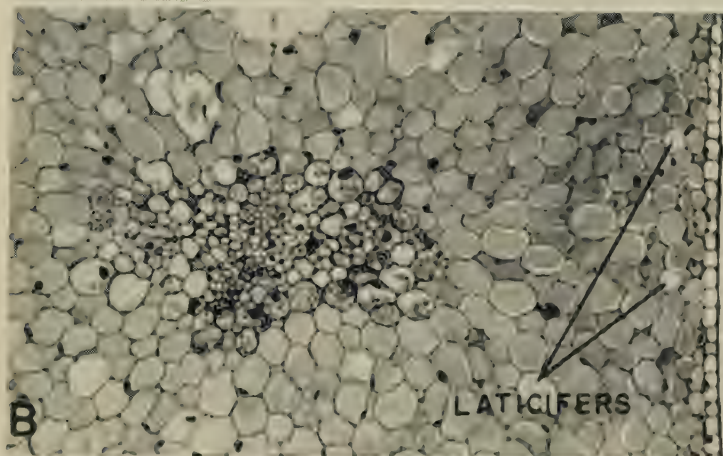


Plate 12. Cross sections of the storage leaf. A is a cleared slice, showing laticifers around the ridge, and the widely distributed vascular bundles. The circles (and small arrow) within the portion delimited by the two radial lines indicate these vascular bundles lacking xylem. B, near outer epidermis, shows a large vascular bundle and the surrounding storage mesophyll. This same bundle, at higher magnification, is shown in plate 13, A. A, $\times 7$; B, $\times 80$.

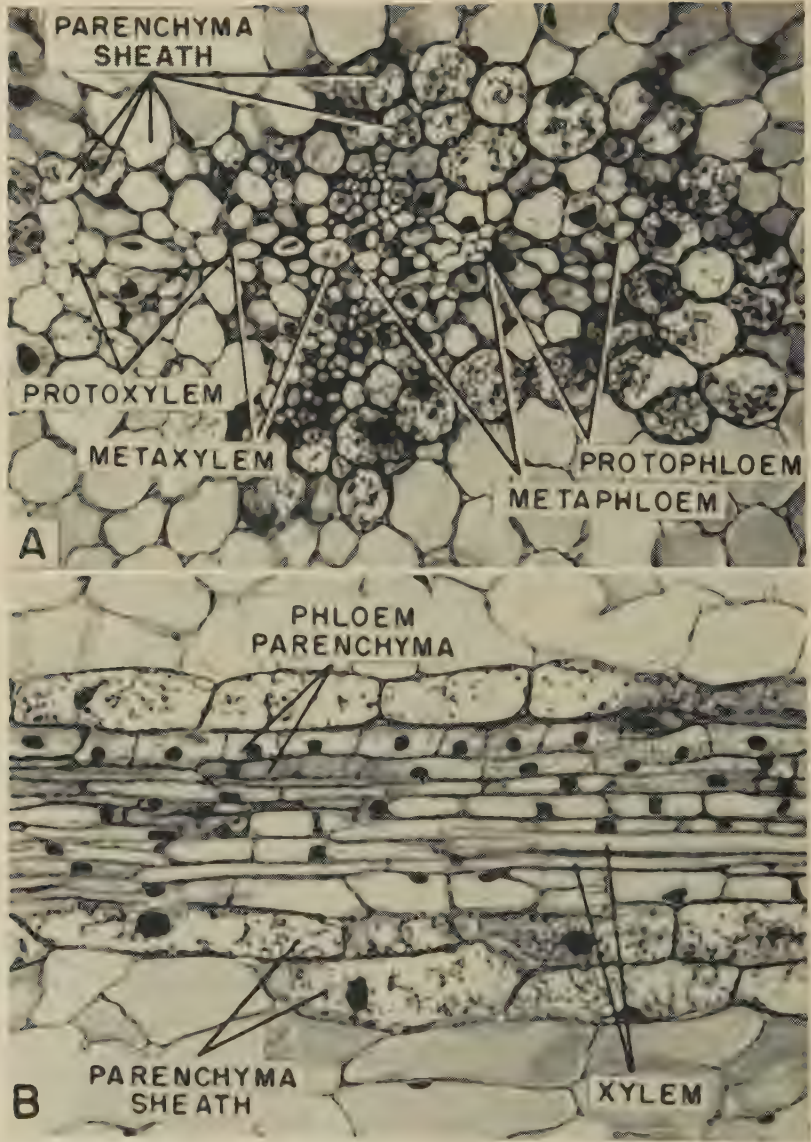


Plate 13. Vascular bundles of the storage leaf. A is one of the large bundles (shown also in plate 12, B) which have areas of crushed protoxylem and protophloem. At B is a long section of a smaller bundle. No crushed protoxylem is present, the elements shown being the oldest in the bundle. Sieve tubes are not visible in the section at B. A, $\times 180$; B, $\times 160$.

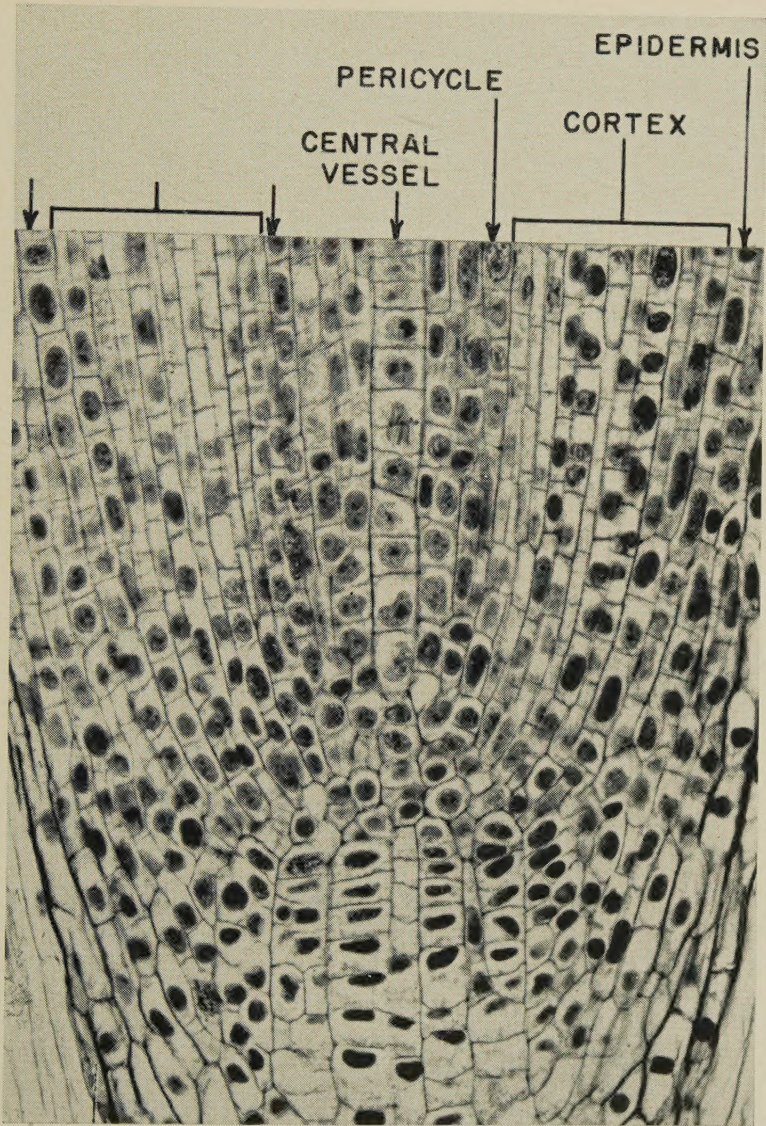


Plate 14. Median longitudinal section of a root tip of garlic showing the meristem and regions derived from it. $\times 360$.

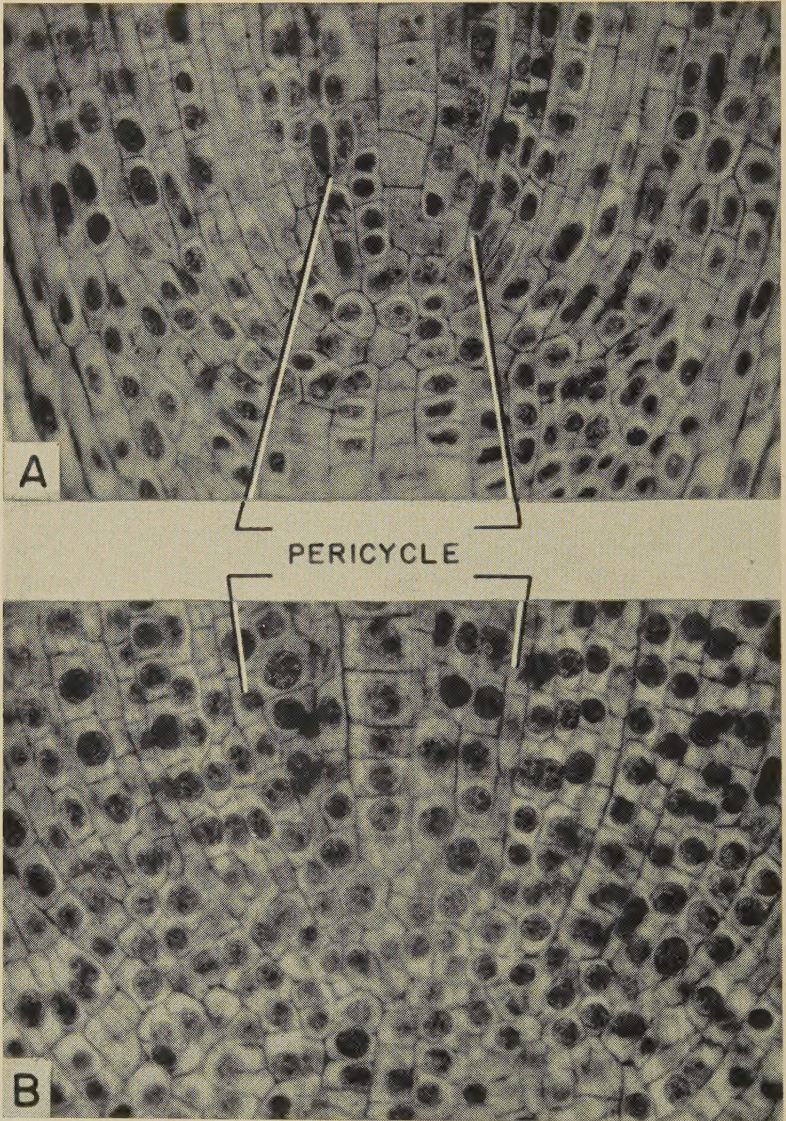


Plate 15. Comparative pictures of the root meristem of garlic (A) and onion (B). The pericycle is labeled to indicate the outer limits of the central cylinder. Both $\times 390$.

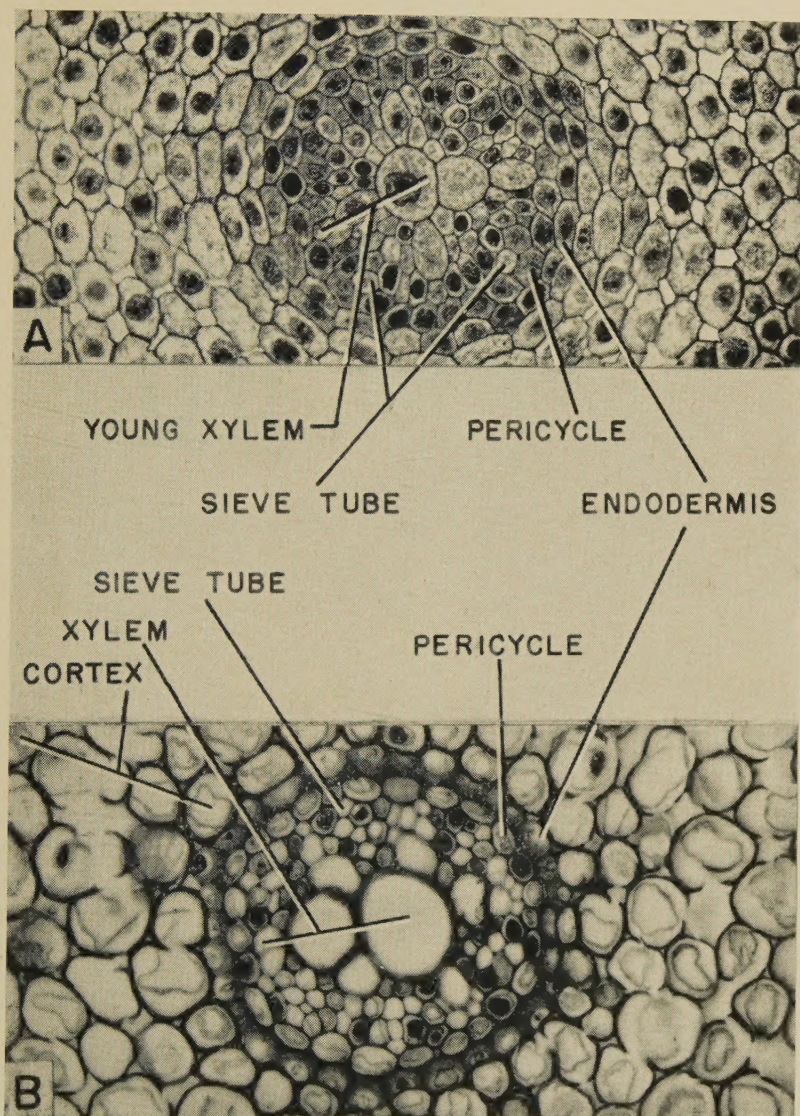


Plate 16. Cross sections of young (A) and mature (B) roots of garlic, showing maturation changes in the central cylinder and adjacent cortex. Both $\times 300$.

